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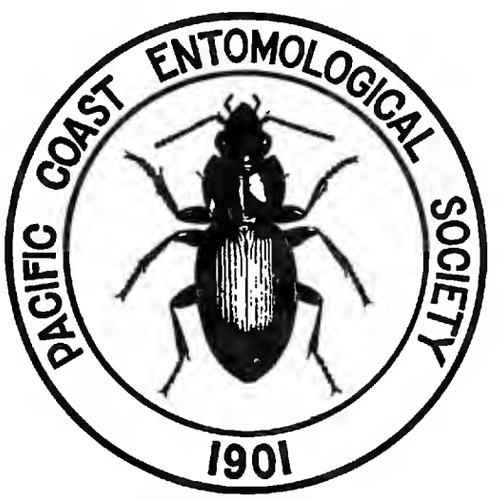

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COLONY FOUNDATION AND PLEOMETROSIS IN *CAMPONOTUS* (HYMENOPTERA: FORMICIDAE)

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The period of reproductive activity and colony foundation is obviously crucial in the life cycle of ants. In most ant species, new colonies are established by independent females after a mating flight. The reproductives are subject to predation and the vagaries of weather during and after the mating flight, and the number of suitable sites for colony foundation available to individual dispersing females may be a limiting factor. The first worker brood is usually reared by the isolated female without any additional assistance. The females might increase the food reserves available for brood rearing by foraging outside the incipient nest, thereby increasing the individual size or number of workers in the first brood, but foraging behavior exposes the female to additional predators. Foraging by colony foundresses occurs only in a small number of ant taxa studied, notably in some Ponerinae and the Australian genus *Myrmecia* (Wheeler, 1933; Haskins, 1955), in some attines (Weber, 1972) and in acacia ants belonging to the genus *Pseudomyrmex* (Janzen, 1966). In most ant species, females do not forage and must rear a worker brood on a limited supply of food reserves. However, conspecific females may cooperate in jointly rearing a first brood; this is termed pleometrosis. Hölldobler and Wilson (1977) provide a recent review of pleometrosis in ants.

Pricer (1908) and Eidmann (1926) provide accounts of colony foundation in two species of *Camponotus* in the eastern United States and Europe. Their studies show that females of *Camponotus ligniperda* and *C. herculeanus* found colonies independently in a manner similar to most other ants. They do not seek food or capture prey outside their incipient nest chamber during colony foundation. *Camponotus* females apparently do not found colonies through temporary social parasitism involving other ant species, unlike some ant genera (Wilson, 1971).

This paper describes colony foundation in seven *Camponotus* species (representing four subgenera) in the western United States. The effect of an initial supplementary feeding on colony foundation success was investigated using two species of *Camponotus*. Five cases of successful colony foundation by pairs of cooperating females of *C. vicinus* are described.

Table 1. Collection data for ants used in study of colony foundation.

Species	No. females	Locality	Date
Camponotus (Tanaemyrmex) vicinus Mayr	1	Tehachapi Mtn. Park, Los Angeles Co., California	July 8, 1973
C. vicinus	4	Iowa Hill, Placer Co., California	May 1974
C. vicinus	7	Iowa Hill	May 1975
C. vicinus	14	Iowa Hill	May 2, 1976
C. (Tanaemyrmex) festinatus (Buckley)	1	Brawley, Imperial Co., California	July 24, 1974
C. (Camponotus) modoc Wheeler	1	Iowa Hill, Placer Co., California	May 1974
C. (Camponotus) laevigatus F. Smith	4	Iowa Hill	May 1974
C. laevigatus	5	Iowa Hill	May 1975
C. laevigatus	1	Flagstaff, Coconino Co., Arizona	May 10, 1974
C. (Myrmentoma) clarithorax Emery	1	Tustin, Orange Co., California	April 24, 1972
C. (Myrmentoma) rasilis Wheeler	2	Victoria, Victoria Co., Texas	May 8, 1974
C. (Myrmentoma) sp.	1	Pinery Valley, Chiricahua Mtns., Cochise Co., Arizona	Aug. 21, 1973
C. (Myrmobrachys) planatus Roger	4	Brownsville, Cameron Co., Texas	June 6–7, 1977

Materials and Methods

The dealate females were collected in California, Arizona, and Texas. Most were taken in the open, presumably at the conclusion of mating flights. Several females were found when the incipient nest chamber was broken open during routing collecting activity. Table 1 lists the collection data for ants used in this study.

Most of the females were housed in 35 mm plastic petri dishes lined with filter paper. Water was supplied periodically to all ants by wetting a cotton ball inserted through the plastic dish lids. The *C. planatus* females were kept in glass shell vials with cork stoppers. The dishes or vials containing founding females were kept together under a thin-wall cardboard box lid or in incubators to exclude light. Air temperatures ranged from 22 to 29°C during colony foundation.

Females collected in 1972, 1973, and 1974 were offered honeywater soon after capture, or as the first larvae neared maturity. In 1975, the effect of this initial feeding was tested using *C. vicinus* and *C. laevigatus*. Three females of each species were denied access to honeywater until the first workers eclosed. Two other females of each species received an initial *ad*

libitum feeding of honeywater shortly after capture. Honeywater was given to all incipient colonies within two days after eclosure of the first worker, and the cotton ball was removed from the petri dish lid to allow ants access to the exterior. Honeywater and insects were supplied on a regular basis once the worker offspring began foraging. Muscid and Calliphorid flies were accepted by most species, and Drosophila flies were taken by *C. clarithorax* and *C.* (*Myrmentoma*) sp. Mealworms (*Tenebrio molitor*) were accepted by *C. vicinus,* which rejected *Drosophila*. The ants and brood later emigrated or were transferred to wood or plaster nests with glass tops.

In 1975, two compatible *C. vicinus* females were placed in one 35 mm plastic petri dish. In 1976, four pairs of compatible *C. vicinus* females were placed in 35 and 60 mm petri dishes (two pairs in each dish size). All dishes and vials with founding females were examined several times each week to monitor the development of the first brood.

Results and Observations

I. Colony Foundation and Effects of Initial Feeding

Nearly all of the dealate females used in this study reared workers to maturity, and required 48 to 74 days to rear the first brood (see Table 2). During colony foundation most of the ants remained motionless for long periods of time (e.g., Fig. 1 is a multiple second time exposure). The females produced a clutch of eggs over a period of several days following installation in the culture containers. The size of this initial egg clutch varied greatly. In the *C. laevigatus* and *C. vicinus* series, the maximum size of the first egg clutch ranged from 9 to 16 for single queen replicates. In the *C. planatus* series, all females produced six eggs or less. The eggs of species in the subgenera *Camponotus, Myrmentoma,* and *Myrmobrachys* were elongate and cylindrical in shape. The eggs of the *Tanaemyrmex* species were broadly oval rather than elongate-cylindrical in shape. The eggs of some species showed striking changes in appearance during embryonic development, due to internal cell movement or migration and changes in the chorion, and eggs of different age could be easily distinguished.

First brood larval growth was usually uninterrupted and rapid. However, the last larvae to hatch in a brood were often 'held back' in the first instar, and usually did not complete development until the following year. The first instar larva is a common resting stage during periods of overwintering or food shortages in *Camponotus* (Mintzer, unpubl. observation; Hölldobler, 1961). In 1974, the *C. modoc* female and three of the *C. laevigatus* females tore loose pieces of filter paper to cover larvae spinning cocoons. Pupal mortality and abortive adult eclosure were uncommon.

The genus *Camponotus* is characterized by a polymorphic worker caste. The workers in the first broods always belonged to the minor subcaste, and

Table 2. Development of first brood during colony foundation.

Species	No. of replicates	Duration of immature stages (days)			Total
		First egg to first larva	First larva to cocoon spinning	First cocoon to first worker	
C. modoc 1974	1	21	13	21	55
C. laevigatus 1974	4	25	14	26	64 (58–69)
C. laevigatus 1975	5	20	12	20	55 (48–70)
C. vicinus 1973	1	22	NR	NR	74
C. vicinus 1974	4	24	14	28	66 (62–70)
C. vicinus 1975	6	21	13	23	58 (54–63)
C. festinatus 1974	1	NR	NR	NR	69
C. clarithorax 1972	1	33	NR	NR	67
C. (Myrmentoma) sp.	1	28 ± 2	14	26	68 ± 2
C. planatus 1977	4	28	12	17	57 (54–58)

showed little size variation. The number of workers produced in the first brood or in the first season varied widely between species, but was often quite similar within a replicate series (e.g., *C. vicinus* in 1974). As expected, the ants aided in tending the brood, but the queen did not abruptly relinquish

Table 3. Effects of an initial honeywater feeding on colony foundation.

Species/female		Treatment	Duration of immature stages (days)			Total	No. of workers + cocoons in first brood (August 15)
			First egg to first larva	First larva to cocoon spinning	First cocoon to first adult		
C. vicinus	BE	fed	20–21	12–14	23–25	58	10
	BF	fed	—	—	—	—	—
	BGX	unfed	25–26	13–14	23	63	10
	BHX	unfed	18–20	12–13	22	54–55	11
	'75	unfed	23	11–12	22–24	57–59	7
	BJX	unfed	17–18	14–15	22–23	55–56	7
Colonies founded by four females receiving initial honeywater feeding in 1974							7, 8, 9, 9
C. laevigatus	AE	fed	20–21	7–8	21	48	8
	AF	fed	18–19	11	18–20	47–50	10
	AGX	unfed	20–21	10–11	22	52	9
	AHX	unfed	19	17–18	19	56	7
	AIX	unfed	41[a]	9	15–21	66–71	4
Colonies founded by four females receiving initial honeywater feeding in 1974							2, 4, 6, 6

[a] Egg consumption by this female probably resulted in the longer egg stage duration observed.

Figs. 1–2. Fig. 1. Colony founding female of *Camponotus vicinus* with first larval brood. Fig. 2. Cooperating pair of *C. vicinus* females with first brood of larvae and cocoons.

brood care after the workers eclosed, and often participated in this activity throughout the first season. Workers in most colonies began foraging within 25 days following eclosure. The foraging workers were generally timid and retreated from any disturbance, although some ants tended to investigate the foraging arena during and after any manipulation, whether or not food was offered. Worker recruitment was occasionally observed in these small colonies during emigration or when honey was offered.

Table 4. First brood egg and worker production by single and paired females (1975, 1976).

		Maximum egg no.	No. of workers and cocoons
Single female	Range	9–16	1–11
Replicates	Mean	12.2	6.8
n = 9	Std. dev.	2.3	3.5
Paired female	Range	17–30	11–17
Replicates	Mean	20.4	13.8
n = 5	Std. dev.	5.5	2.6

Table 3 shows the results of the experiment testing the effect of initial feeding on colony foundation. One of these ants (female BF) was infertile and her eggs failed to hatch, even though she had received honeywater. All other ants reared brood to maturity. Egg eating was not observed among females which had received honeywater, although unaccounted loss of eggs was noted in one case (female AE). Egg eating by two unfed ants (AIX and BJX) was observed, and one egg was consumed in each case. One pupa disappeared and was presumably consumed by an unfed *C. laevigatus* female (AGX). The maximum size of the egg clutch was similar in the two groups, as was the brood development time and the number of workers in the first brood.

II. Cooperative Colony Foundation by Two Females

In 1975, a pair of *C. vicinus* females successfully reared a brood of 11 workers to maturity. The two ants maintained a single egg pile; the maximum size of this clutch was 21 eggs. In 1976, four pairs of *C. vicinius* successfully reared worker broods to maturity. Several pairing attempts were required to find compatible females for this experiment, as some combinations of the ants available led to fighting. One female lost three legs in such fights after initial pairing. However, paired females that were compatible in the initial stages during egg laying remained compatible for the entire period of colony foundation. Oral food exchange between females and allogrooming was observed, and 'dominance' or aversive behavior was very subtle or absent. Occasionally one female would climb partially on top of the second female, but biting was never observed (cf. *Polistes*; West-Eberhard, 1969) and the putative dominant-submissive roles were often reversed when the behavior was observed again. On May 21, an accident resulted in the loss of all eggs in the dishes, but all of the ants produced a second clutch. The paired females produced a single egg clutch, which was larger ($p < 0.01$, Behrens-Fisher t test) than the egg clutches of single foundress queens. The time period involved and the details of brood development were similar in single and paired-female series, but paired females produced

more workers than single females ($p < .005$, Behrens-Fisher t test). Females in 60 mm dishes did not rear more workers than did those in 35 mm dishes.

Three of the four pairs of females founding colonies in 1976 remained compatible through August 1977. One pair was separated after fighting between the females began in March 1977. The largest colony with two females had 42 worker offspring in early August 1977.

Discussion

The high proportion of females which successfully founded colonies is noteworthy. The culture dishes and vials satisfied a requirement for a small closed cavity during colony foundation, without contamination by pathogenic bacteria and fungi. The four subgenera of *Camponotus* surveyed in the study occupy different habitats in nature. Ants in the subgenus *Tanaemyrmex* nest in the soil in the western and southern United States. *Camponotus laevigatus* and *C. modoc* occur in forested mountain areas in western North America, and nest in large pieces of wood. The ants in the subgenus *Myrmentoma* are largely arboreal and are distributed throughout the United States and southern Canada. The subgenus *Myrmobrachys* is the dominant group of arboreal *Camponotus* in neotropical habitats, and occurs in the United States in southern Arizona, Texas, and Florida (Creighton, 1950).

Conditions in the laboratory probably minimized the brood development time. Water was supplied on a regular basis, and temperature extremes were avoided during colony foundation. Under these conditions, supplemental honey feeding had little or no effect on the first brood development time, and did not appear to increase the size of this brood. Brood cannot be satisfactorily reared on honeywater alone. However, the ants could use the sugars present in honey for some of their own metabolic needs, and thereby free more protein and lipid reserves for use in brood rearing. Such a facilitatory effect has been demonstrated in *Myrmica* (Brian, 1973). Under less satisfactory culture conditions, beneficial effects of the initial feeding might become apparent. Brood consumption was uncommon in the laboratory, but was more frequent among unfed females. In the field, lower average or fluctuating temperatures would probably prolong or interrupt brood development, especially in areas inhabited by *C. modoc* and *C. laevigatus*.

The successful foundation of colonies by pairs of cooperating *Camponotus* is significant. Only one other account (Stumper, 1962) of pleometrotic colony foundation by *Camponotus* females is available. Stumper's colony foundation experiments with *C.* (*Camponotus*) *vagus* Scopoli were plagued by a high level of brood cannibalism and none of his single-female replicates reared workers to maturity. However, his pair of compatible females was successful at rearing workers, and produced more brood than the single females. Paired or grouped females of *Lasius flavus* (Fabricius) rear more

brood to maturity in a shorter period of time, and have a higher survivorship rate than single females (Waloff, 1957). Pairs of compatible *C. vicinus* founding females also appear to rear larger broods than single females. It is not clear whether both females are contributing brood during colony foundation. Even if only one individual in a pair contributes eggs to the clutch, she can produce a correspondingly larger number of eggs, to be tended by two founding females. However, the origin of these eggs probably will not influence the ultimate reproductive success of cooperating females. The reproductive success of each female is determined by the number of reproductive females and males contributed by each when the colony reaches maturity, and by colony survivorship functions. The increased number of workers produced by paired females may have a major positive impact on survivorship of incipient polygynous colonies. Unrelated females may be expected to cooperate if their expected reproductive success is increased above the level for haplometrotic colony foundation. According to kin-selection theory, related females may be expected to cooperate in colony foundation under some conditions when unrelated females would not, as long as the inclusive fitnesses of the participating ants are increased (Hamilton, 1964). All of the *C. vicinus* females involved were collected in a single locality and it is possible that some are sisters. The behavior of the ants during pairing attempts suggests that they are discriminating on some basis, possibly residual odor cues from the parent colony.

Records of mature polygynous colonies of *Camponotus* in nature are uncommon. Hölldobler (1962) found some in *C. ligniperda,* where the females were hostile to each other and maintained separate territories in large colonies. In a series of experiments, he found that newly fertilized dealate females were usually incompatible, and those females which did cooperate failed to rear a first brood to maturity. Hölldobler concluded that polygynous colonies of this ant arise by adoption of females or mating within the colony. In August 1973, the author excavated a large colony of *C.* (*Tanaemyrmex*) *sansabeanus* (Buckley) with two dealate females near the Southwest Research Station of the American Museum of Natural History at Portal, Arizona. These ants have shown no aggressive behavior towards each other in the four years after collection of this colony. Both contribute eggs and egg eating by the queens has not been observed. It seems likely that polygynous colonies of this type could occasionally originate through cooperation between founding females.

Conclusion

Under laboratory conditions, *Camponotus* females required 48 to 74 days to rear a worker brood to maturity. The development of this brood was uninterrupted and supplemental honeywater feeding did not accelerate de-

velopment or increase the brood size. Queens of *Camponotus vicinus* may cooperate during colony foundation; females doing so increased the size of the first worker brood, although the development period was not appreciably shortened.

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ALFALFA LEAFCUTTER BEE—REDUCING PARASITISM OF LOOSE CELLS DURING INCUBATION (HYMENOPTERA: MEGACHILIDAE)

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The alfalfa leafcutter bee, *Megachile pacifica* (Panzer), is the most commonly used pollinator of western alfalfa seed fields. One method of increasing these bees entails removing their leaf cells from nesting media in the fall and cold-storing them until spring. Bees are obtained by incubating the cells for approximately 20 days at 85°F (30°C). Often some cells are parasitized by chalcid wasps (*Monodontomerus*—an external parasite, *Tetrastichus*—an internal parasite), and since the parasites emerge 11–12 days after beginning incubation of the bees, they have amply opportunity to parasitize many additional host cells before bee emergence occurs. Various types of light traps or cell coverings have been used to reduce parasitism (Waters, 1970; Hobbs, 1973; and Johansen et al., 1973), but none of these methods is satisfactory. Recently Brindley (1976) recommended dipping cells in carbaryl insecticide to reduce parasitism. Some growers have sprayed insecticides on loose cells during incubation, but information on bee kill or parasite control has not been recorded. Because these insecticide control methods employ toxic agents and are not commonly used, methods to repel parasites before parasitism occurred were tested.

Methods

Thirty-three groups (150 cells each) of leafcutter bee cells were placed in covered 6-oz plastic cups and incubated at 90°F for 10 days. Before parasite emergence the cells were removed from the incubator. *N, N*-diethyl-*m*-toluamide (deet) (99.6% stock) was diluted in 20% sugar water to prepare 0, 2, 6, and 18% repellent solutions. Four groups of cells were dipped for 5 sec in each of the four repellent solutions (4 treatments, replicated 4×). The cells were air-dired at 32°C for 3 hr in the greenhouse. In a second test vermiculite pieces (1–3 mm) were soaked for 10 sec in each of the 4 repellent solutions and air-dried as were the leafcutter bee cells. Four groups of cells were mixed and covered with 3 mm of dried, treated vermiculite (4 treatments, replicated 4×).

The last group of incubated cells was isolated individually in gelatin capsules (1 group, 1 replication). This treatment was necessary to provide con-

trol bees for the last part of these tests. Then, all cell groups in each treatment were replaced in cups and returned to the incubator.

Four other cell groups (150 cells each) used as a control, were dissected and their contents were recorded. This group came from the same stock bee population that was held in cold storage, and it provided data on the incidence of parasitism in the stock bees.

Parasite and bee emergence in the treatments were recorded 3×/day (8, 11, 16 hr). The parasites were left in the plastic cups, but the bees were removed during each observation period. One hundred bees (50 ♂♂, 50 ♀♀) from each treatment were placed in large covered cages (in the greenhouse) and fed a 20% sugar-water solution. Dead bees were recorded and removed from the cages daily to assess longevity of bees emerged from each treatment. After all parasites and bees had emerged, cells without exit holes were dissected and their content were recorded.

Results

Deet-treated cells.—*Tetrastichus* began to emerge from the cells on the 11th day, and *Monodontomerus* emerged on the 12th day of incubation. The *Tetrastichus* in the 0% test remained active, mating and crawling about the cells for 13 days, whereas these parasites in the 2, 6, and 18% repellent treatments concentrated beneath the lids and away from the cells. The *Tetrastichus* population in the repellent treatment cups began to decline 4 days after emergence; no parasites were alive 8 days after emergence. *Monodontomerus* reacted similarly but often crawled about the cells in all the cups.

Cells treated with repellents had significantly greater bee emergence than the 0% treatment, in which no bees emerged. The number of bees exiting cells was highest in the 6% treatment (Table 1). However, parasite emergence was significantly lower in the repellent-treated cells than in the 0% treatment. Also, parasite emergence was lower in the 18% treatment (9.1%) than emergence in the gelatin capsules (21.3%) and emergence in the dissected controls (22.8%). Also, a significantly higher number of dead cells was found in the 18% deet treatments. Apparently this treatment killed some of the bees and parasites during incubation.

Vermiculite-covered cells.—Parasite activity in this test was similar to that observed in the deet treatments; namely, parasites in the cups with repellent concentrated under the lids and away from the vermiculite. The emergence and death rate of the parasites were similar.

As with the deet-treated cells, significantly more bees emerged in the treatments with repellents than in the 0% treatments. Emergence was greatest in the 6 and 18% treatments and significantly higher than emergence in the 2% treatment. However, cells in gelatin capsules had some mortality,

Table 1. Effect of vermiculite and deet treatments on emergence of alfalfa leafcutter bees and parasites, Logan, Utah, 1977.

Treatment		Live bees		Live parasites		Dead cells	
		Avg. no.	%	Avg. no.	%	Avg. no.	%
Vermiculite:	0%	0.00	(0.00)a[1]	79.00	(52.60)a	70.50	(47.00)a
	2%	73.50	(48.70)b	42.00	(28.00)b	29.00	(19.30)b
	6%	82.25	(54.60)c	33.75	(22.50)b	29.25	(19.50)b
	18%	87.75	(58.00)c	35.00	(23.30)b	23.00	(15.30)b
Deet:	0%	0.00	(0.00)a	80.00	(53.30)a	67.75	(45.20)a
	2%	60.50	(40.30)b	39.50	(26.33)b	48.50[2]	(32.30)b
	6%	85.00	(56.70)c	29.50	(19.66)c	30.75	(20.50)c
	18%	35.25[2]	(23.50)d	13.75[2]	(9.10)d	94.25[2]	(62.80)d

[1] Numbers followed by the same letter are not significantly different ($P < .05$).
[2] Significant difference between vermiculite and dipped treatments ($P < .05$).

probably because of desiccation, since 14% of these cells contained dead, but fully formed adults. If these values are combined, the 47.3% emergence rate plus the 14% dead adults (61%) in the gelatin capsules approximates the emergence rate observed in the 18% repellent treatment (58%). However, significantly lower levels of parasite emergence were found in the repellent treatment all of which were similar (Table 1). Also, the number of dead cells was significantly lower in the repellent treatments (15.3–19.5%) and similar to the number of dead cells found in the gelatin capsules (16.6%).

Caged bees.—The longevity of bees emerging from 2% repellent treatments was similar to that of bees emerging from the gelatin capsule treatment (Fig. 1). Longevity of bees from the 6% dipped cells was also similar, but the bees from the 6% vermiculite had a slightly higher death rate (Fig. 1). The highest death rate was observed in bees from the 18% dipped and vermiculite treatments (Fig. 1). All bees died 20 days after emergence because of uncontrolled, high greenhouse temperatures.

Discussion

The results of these tests indicate that the repellent treatments significantly reduced parasitism during incubation of loose cells and thereby increased bee emergence. The 6% deet treatment appeared to cause the highest bee emergence, with longevity about equal to that of untreated bees. It was a surprise to observe a higher death rate for bees emerging from the vermiculite, since higher death rates were not observed among the immature stages during the test. Several factors could have contributed to this higher

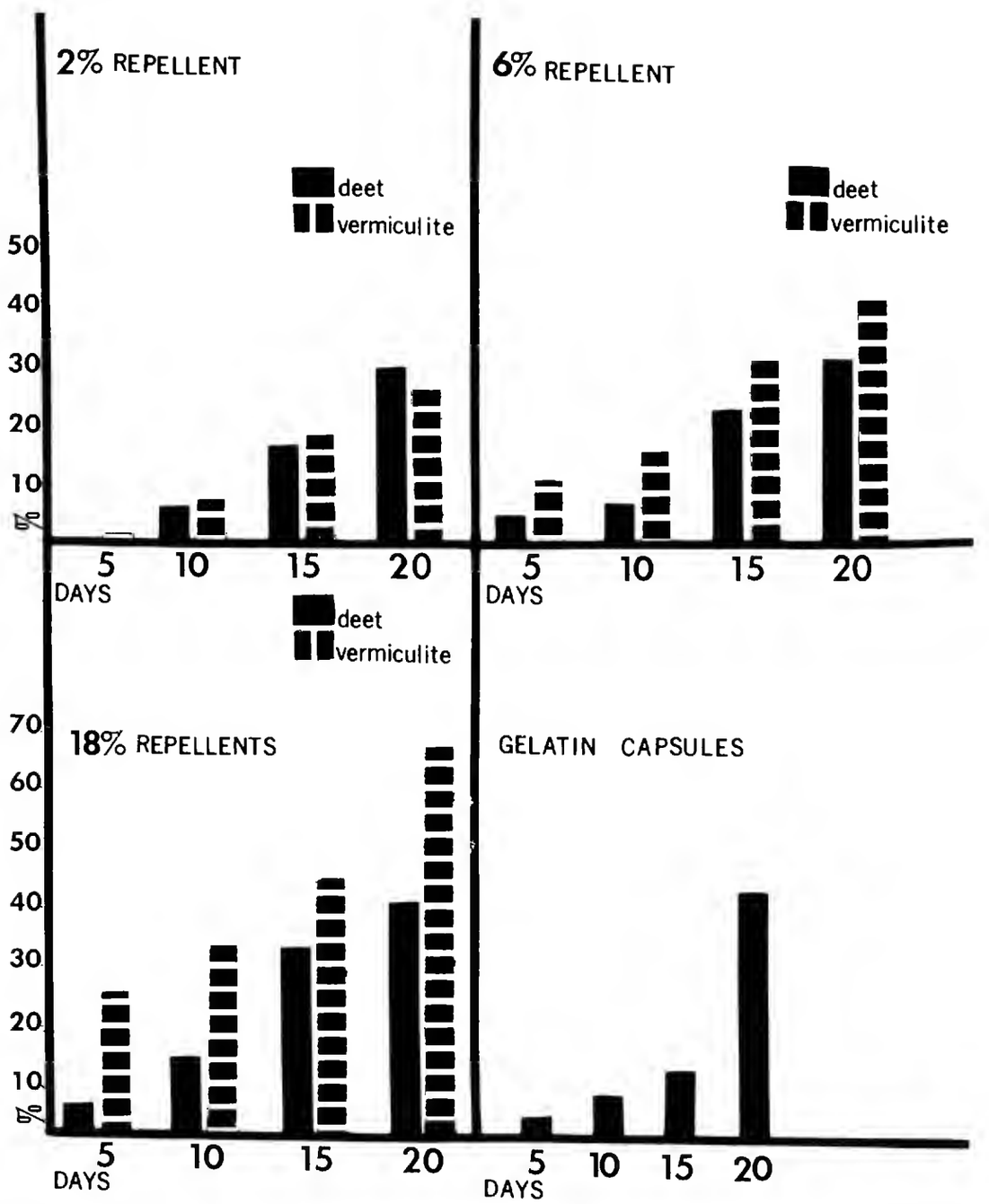

Fig. 1. Cumulative percent death of adult *Megachile pacifica* in repellent treatments.

rate. First, the bees were confined in the small cups for several hours after their emergence. In a commercial operation they could easily escape soon after emergence. Also, the vermiculite may have absorbed and concentrated the deet since the repellent odor was very strong when the vermiculite-covered cells were opened.

In laboratory tests an aerosol repellent works very well in large incubators where blue-black lights are used over pans of soapy water. The repellent keeps the parasites away from the cells, and they are more readily attracted to the light traps. I have sprayed loose cells of our laboratory colony with repellent for the past 2 seasons and practically eliminated parasitism during

incubation. Bees emerging from our sprayed cells have nested adequately; their population has increased by over 2-fold each season.

Aerosol repellents are available from several commercial sources, with concentrations of active ingredients ranging between 6 and 12%. The concentration of active ingredients in the aerosol used to spray our laboratory colony was 71% (Stock No. 6840-00-082-2541, General Services Administration, Federal Supply Service, Washington, D.C. 20406). The differences between the results noted in these tests and those observed in our sprayed laboratory colony of leafcutter bees may have been caused by a dilution factor. The amount of applied active ingredient in an aerosol is much less than in the repellent solutions used to dip cells. Therefore, it may be necessary to use a higher concentration of active ingredients if aerosol sprays are used.

Acknowledgments

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ORIGINS OF PSYLLID FALLOUT IN THE CENTRAL SIERRA NEVADA OF CALIFORNIA (HOMOPTERA)

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Psyllidae (Insecta: Homoptera) make up a major proportion of the wind-blown (aeolian) insect fauna deposited on alpine snowfields in the Sierra Nevada of California (Papp, 1975). During the summers of 1972 to 1974, 1206 psyllid specimens comprising 18 species in six genera were collected on névé snow at 3353 m on Mt. Conness in the Inyo National Forest. Since psyllids are an important food for nival aeolian zone predators and scavengers (Papp, 1978), knowledge of their origin is basic to understanding the dynamics of energy flow into the aeolian ecosystem as well as details of the intrasystem community structure.

Four species of Psyllidae (*Psylla hirsuta, P. magna, P. alba* and *Aphalara artemisiae*) accounted for 93.2% of the total psyllid fallout on Mt. Conness snowfields (Table 1).

At least 14 other species were taken on snow during 1972–74, including some species taken only once. Among these were the widespread pear psylla, *Psylla pyricola* Forster. Hagen (1976, personal communication) has taken this species at high altitudes in the Alps. Another species, *Paratrioza cockerelli* (Sulc) has many solanaceous hosts, including potato and tomato. A complete listing of aeolian psyllids is given in Table 2.

Distribution of the hostplant species for the four common psyllids collected on Mt. Conness snow are given in Table 3. Four species, *Cercocarpus betuloides, Corylus cornuta, Salix melanopsis* and *Salix Hindsiana,* are found only on the west slope of the Sierra Nevada, and none occur above

Table 1. Common psyllids collected on Mt. Conness snowfields, 1972–74.

Species	Specimens collected			Total	% of total
	1972	1973	1974		
Psylla hirsuta (Tuthill)	0	107	165	272	22.6
Psylla magna Crawford	0	245	30	275	22.8
Psylla alba Tuthill	1	453	20	474	39.3
Aphalara artemisiae complex	0	21	82	103	8.5
Other spp.	3	15	64	82	6.8
Total	4	841	361	1206	100.0

Table 2. Aeolian Psyllidae collected on Mt. Conness, 1972–74.

Species	Host(s)
Aphalara calthae complex	*Polygonum* spp., *Artemisia tridentata, Caltha palustris,* others
Aphalara minutissima Crawford	*Artemisia tridentata*
Aphalara veaziei metzaria Crawford	*Achillea millefolium,* other Compositae
Euphalerus vermiculosis Crawford	*Ceanothus* spp., *Lupinus* sp.
Livia juncorum Latreille	*Juncus, Carex, Pinus*
Paratrioza cockerelli (Sulc)	*Solanaceae,* inc. *Solanum tuberosum* (potato) and *Lycopersicon esculentum* (tomato)
Psylla alba Crawford	*Salix melanopsis, S. Hindsiana, S. Hindsiana* var. *sessilifolia, Cercocarpus ledifolius*
Psylla breviata Patch	*Salix*
Psylla hirsuta (Tuthill)	*Cercocarpus ledifolius, Purshia tridentata, Corylus cornuta*
Psylla insignita Tuthill	*Cercocarpus ledifolius*
Psylla magna Crawford	*Cercocarpus ledifolius, C. betuloides,* "Serviceberry" (prob. *Amelanchier*)
Psylla magnacauda Crawford	*Shepherdia argentea, Eleagnus* sp.
Psylla media Tuthill	*Cercocarpus ledifolius, C. betuloides*
Psylla minor Crawford	*Salix californica, S. lasiolepis*
Psylla pyricola Forster	*Pyrus communis* (pear)
Trioza incerta Tuthill	*Salix*
Trioza sp. (*singularis*?)	unknown

2500 m in California. The other hostplants, *Cercocarpus ledifolius* and *Purshia tridentata,* are distributed along the east slope of the Sierra Nevada at altitudes ranging up to 3200 m. While climatological data show that prevailing winds across the Sierra are primarily from the west, southwest, or south (96%, 69%, 88% in 1972, 1973, 1974 respectively) in late spring and early summer, turbulence resulting from high velocity winds blowing across the Sierran crest also create diurnal anabatic (upslope winds) from the eastern deserts. It is therefore apparent that psyllid fallout along the crest of the Central Sierra Nevada has at least two origins: a major component from the Central Valley and the west slope (aeolian transport by geostrophic winds), and a minor component from the Owens Valley and east slope (aeolian transport by anabatic winds originating in the deserts leeward of the Sierra Nevada).

Table 3. Distribution of common psyllid hostplants. (Data from Munz, 1959, 1968.)

Hostplant (Psyllidae)	Distribution
Cercocarpus ledifolius Nuttall (*Psylla hirsuta, P. alba*)	Dry, rocky slopes along the east side of the Sierra Nevada at 1220–3200 m; also in mts. of W Mojave Desert and N to Modoc and Siskiyou Cos.; to E Washington, Montana, Colorado, Arizona, Baja California.
Cercocarpus betuloides Nuttall (*Psylla magna*)	Chaparall and oak woodlands along the W slope of the Sierra Nevada below 1830 m; also cis-montane California to SW Oregon; N Baja California.
Purshia tridentata (Pursh) DeCandolle (*Psylla hirsuta*)	Dry slopes along east side of Sierra Nevada at 900–3200 m; also in the White Mts.; in California ranges from Tulare and Inyo Cos. N to Modoc, Siskiyou and Trinity Cos.; thence to Lake Co., British Columbia, Montana, New Mexico.
Corylus cornuta Marsh (*Psylla hirsuta*)	Damp slopes and banks, below 2200 m, in many plant communities; in the Coast Ranges from Santa Cruz Co. N, and in the Sierra Nevada from Tulare Co. N; to British Columbia.
Salix Hindsiana Benth. (*Psylla alba*)	Common locally among ditches, on sand bars, etc., below 3000 ft; many plant communities; cis-montane California, into Oregon and Baja California.
Salix Hindsiana Benth. var. *leucodendroides* (Rowlee) Ball. (*Psylla alba*)	Sparingly in Santa Clara and Tulare Cos. to Kern Co.; more common Ventura to San Diego Cos. to Baja California.
Salix melanopsis Nutt. (*Psylla alba*)	Stream banks below 8000 ft; many plant communities; Sierra Nevada N to Modoc County, coast ranges from Lake and Sonoma Cos. N; to British Columbia; Rocky Mountains.

Sierran alpine predators and scavengers which are able to withstand the rigors of nival foraging are thus able to take advantage of aerial plankton fallout originating from at least two directions: the forest and riparian biomes to the west, and the pinyon-sagebrush biomes to the east.

Acknowledgments

The host and distribution data for Psyllidae were taken from California Insect Survey specimen data and from unpublished notes of the late Dr.

Dilworth Jensen, formerly of the University of California, Berkeley. Appreciation is expressed to the U.S. Forest Service for permission to conduct research in the Harvey Monroe Hall Natural Area, to the Carnegie Institution of Washington for use of the Timberline Station facilities, and to the Division of Biological Control at the University of California, Berkeley for partial financial support during field research.

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Footnote

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A NEW SPECIES OF *PHANAEUS* FROM MEXICO (COLEOPTERA: SCARABAEIDAE)

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Phanaeus is a New World genus of dung beetles well known for bright, metallic colors and striking sexual dimorphism. The purpose of this paper is to describe a new Mexican species with unusual ecological characteristics. The primary geographical center of diversity of *Phanaeus* is tropical Mexico (Edmonds, 1972). Rather than to Mexican groups, however, the new species is more closely related to those Central and South American species which comprise the *P. splendidulus*-group (Edmonds, 1972). Of these species, it is most closely related to *P. endymion* Harold, the only other member which also occurs in Mexico.

Phanaeus halffterorum, new species
(Figs. 1–3, 6–8)

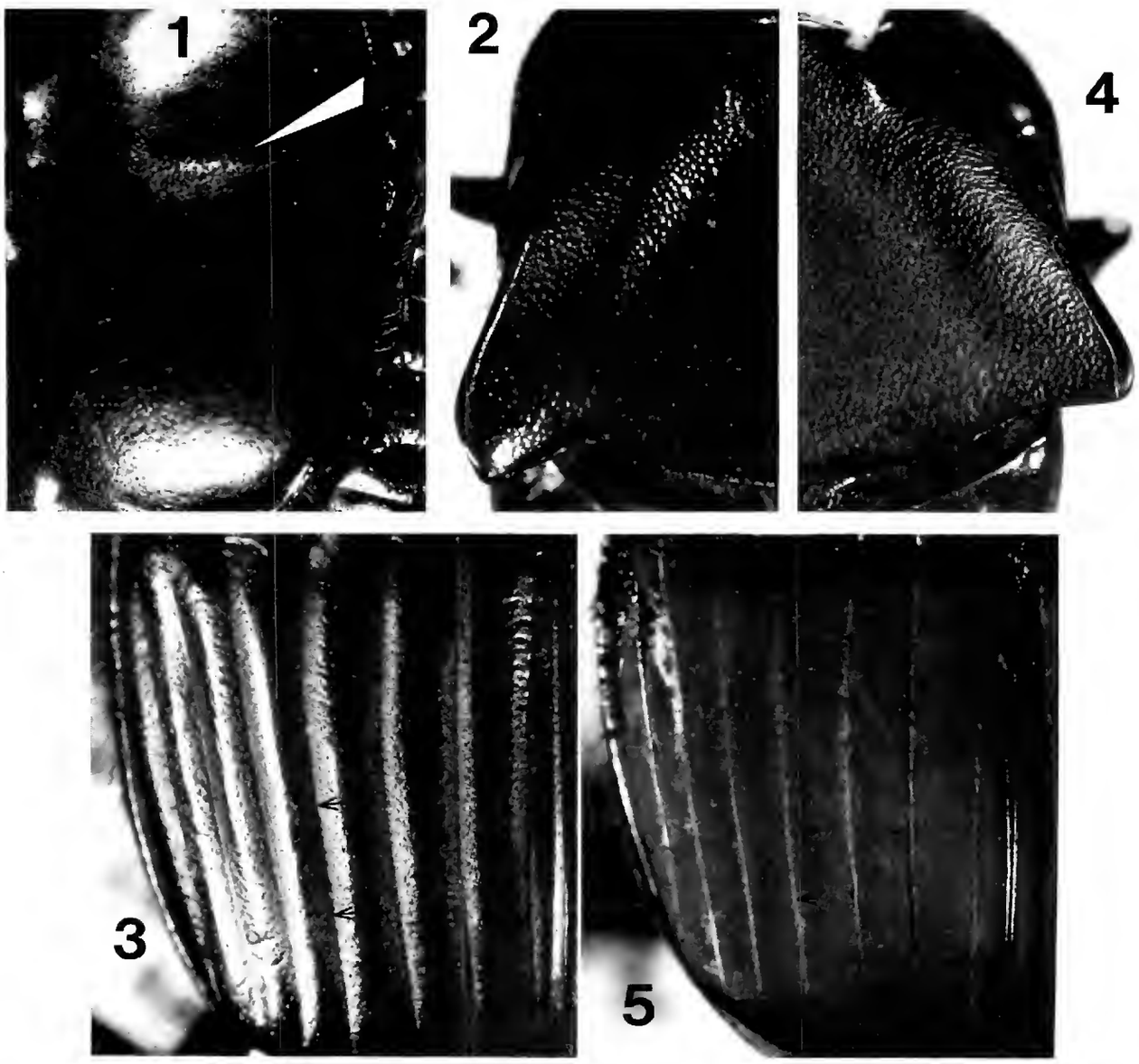
Holotype.—Male, Mexico, state of Mexico, 8 km W Temascaltepec, 2360 m, VII-11-76, fungus in pine-oak forest, W. D. Edmonds, P. Reyes and B. Kohlmann.

Paratypes.—3 males, 2 females, same data as holotype; 4 males, 4 females (1 designated allotype), 5 km E Temascaltepec, Real de Arriba, 2200 m, VII-10-76, fungus in oak-pine forest, W. D. Edmonds, P. Reyes, B. Kohlmann; 1 male, 1 female, 5 km W Temascaltepec, 2200 m, fungus in oak-pine forest, VII-23-77, W. D. and T. B. Edmonds; 1 male labeled "Real de Arriba, VII-1932, 6300 ft, Mexico D. F., Hinton coll., BM 1939-583"[1]; 1 male labeled "Mex. Guerrero, 22 mi S Chilpancingo, 2800 ft, VIII-2-1964, Richard D. Page, col."

Disposition of types.—Holotype and allotype—California Academy of Sciences, San Francisco (CAS Ent., Type 13184); 1 pair paratypes—British Museum (Natural History), London; 1 pair paratypes—Halffter collection, Mexico City; 1 male paratype—United States National Museum, Washington, D.C.; 1 male paratype—A. Martínez collection, Buenos Aires; remaining paratypes—temporarily in my collection.

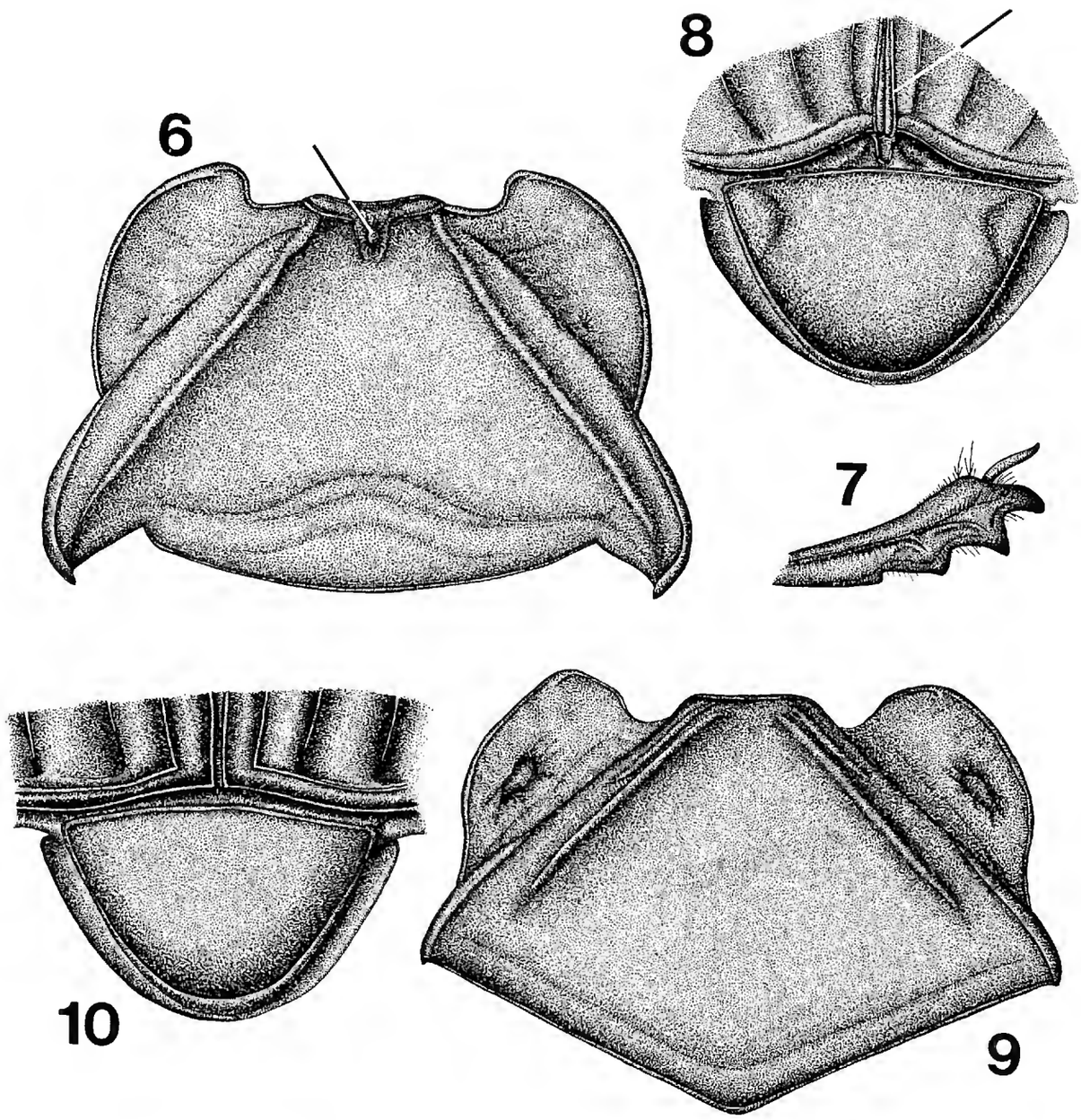
Derivation of epithet.—From the surname Halffter. It is my pleasure to dedicate this species to my very good friends and colleagues, Gonzalo Halffter and his lovely wife Violeta M. de Halffter, in recognition of their many contributions to the study of Scarabaeinae.

Major male.—Dorsum dark, shining, iridescent green or dark blue (iri-



Figs. 1–5. Figs. 1–3. *Phanaeus halffterorum*: Fig. 1—dorsal view female pronotum (arrow indicates mid-dorsal depression); Fig. 2—dorsal view left side male pronotum; Fig. 3—dorsal view left elytron of male (arrows indicate 4th stria). Fig. 4—*Phanaeus endymion,* dorsal view right side male pronotum. Fig. 5—*Phanaeus funereus,* dorsal view left elytron of male (arrow indicates 4th stria).

descence subdued on elytra) except outer margin of head, cephalic process ("horn"),[2] posterior part of head and lower surface of posterior pronotal angles, which are shining black; venter red-brown to chocolate-brown except abdominal sterna, middle and hind femora and pteropleura, which are tinged with green (or blue). Clypeus distinctly bidentate, teeth rounded; subclypeal process transverse. Cephalic process long, tapering, curved evenly posteriorly over pronotum. Prothoracic disk (Fig. 6) triangular, flattened but with distinct undulations laterally and posteriorly; posterior angles very salient, directed posterolaterally and slightly upturned apically; middle of anterior margin with a strong, acute tooth (except Guerrero specimen);



Figs. 6–10. Figs. 6–8. *Phanaeus halffterorum,* male: Fig. 6—dorsal view pronotum (guideline indicates anterior tooth); Fig. 7—right front tibia; Fig. 8—caudal view tips of elytra, pygidium and 8th abdominal sternum (guideline indicates raised inner margin of elytron). Figs. 9–10. *Phanaeus endymion,* male: Fig. 9—dorsal view pronotum; Fig. 10—caudal view tips of elytra, pygidium and 8th abdominal sternum.

pronotum distinctly granulate dorsally (Fig. 2), granulation, while better appreciated under magnification, visible as fine texturing (like that of sandpaper) to unaided eye; sculpturing becoming punctate posteriorly and progressively more clearly punctate and less granulate anterolaterally; disk shagreened and highly shining. Front tibia quadridentate (Fig. 7). Elytra (Fig. 3) with very fine, simple striae, interstriae distinctly convex medially such that striae lie in longitudinal furrows; inner margin a ridge progressively more raised and keel-like posteriorly which extends beyond apical margin of elytron as rounded tooth (Fig. 8); lateral margin of elytron distinctly

excised apically adjacent to inner margin. Pygidium (Fig. 8) weakly to moderately punctate, punctures usually coalescent at least medially; each side with shallow elongate depression.

Minor male.—As above except as follows: Cephalic process shorter, more upright or reduced to a simple tubercle; flattened, triangular shape of pronotum much less pronounced, posterior angles reduced to tubercles well anterior to posterior margin, anterior tooth absent.

Female.—As above except as follows: Cephalic process a trituberculate, transverse carina extending between ends of postclypeal carinae; most of pronotal disk shining black, green color not iridescent (blue phase known in male only). Pronotum evenly covered dorsally with shallow punctures, appearing very smooth to unaided eye; puncturing sometimes effaced medially and coalescing laterally to produce weak rugosity; surface not shagreened, coloring (where present) less brilliant than in male; strongly convex, bearing weakly raised anterior transverse ridge with three isolated tubercles followed by shallow concavity; distinct mid-longitudinal depression extending from posterior margin to near middle of disk (Fig. 1, arrow).

Size.—Length 12–19 mm; width (at bases of elytra) 8–12 mm.

Habitat and distribution.—Temperate oak-pine/pine-oak forests ordinarily above 1900 m along southern slopes of the Transverse Volcanic Range and in the highlands of Guerrero, Mexico; feeding on wild mushrooms; probably active at dusk and early evening hours.

Discussion

This species is the same mentioned by me in 1972 as *incertae sedis* (p. 830); females, which were not available then, indicate without doubt that *P. halffterorum* is a member of the *endymion*-complex of the *P. splendidulus*-group. Pronotal sculpturing of the male, however, requires that the second alternative of the first couplet of my key to the species groups and complexes of *Phanaeus* (p. 829) be modified partially to read as follows: ". . . or minutely to distinctly granulate or granulorugose (males of *endymion* complex) . . . ." *P. endymion* differs from *halffterorum* by the following combination of characters, the counterparts of which are included in the above description: the color is weakly shining green or blue and never highly iridescent on the head and pronotum of the male; most of the disk of the female is colored, less of it is black; the pronotum of the large males (Fig. 10) is more broadly triangular, very flat, and the posterior angles are less salient and directed laterad; even the largest males are without a trace of an anterior pronotal tooth; the pronotum of the female has at most a fine mid-dorsal, longitudinal line on the posterior part of the pronotum and is never distinctly impressed along this line; the disk of the male pronotum (Fig. 4) is at most only weakly granulorugose, appearing virtually smooth

to the unaided eye and, seen under magnification, often with minute widely spaced, shining punctures in a field of effaced granules and weak shagreening; the inner margin of the elytron is not ridge-like, lacks an apical tooth and is not excised (Fig. 10); the pygidium (Fig. 10) lacks indications of lateral depressions; the species inhabits lowland evergreen and deciduous forests of eastern and southeastern Mexico and Guatemala below 800 m, feeds on excrement of non-herbivores and, occasionally, carrion; active during early morning hours.

The most useful morphological features for distinguishing *halffterorum* from other members of the complex are the shape and sculpturing of the male pronotum and the strong ridge along the inner margin of each elytron. Most groups of *Phanaeus,* including the *endymion*-complex, are in need of revision. I have insufficient data to reliably distinguish among the other, currently recognized members of the complex, *blanchardi* Olsoufieff, *funereus* Balthasar, and *pyrois* Bates, all of which are from Central or northwest South America and presumed to be reasonable taxonomic species. Collectively, however, these three species differ from *halffterorum* and *endymion* by the following characters: the elytral interstriae are relatively flat, the striae are very fine and not lying in pronounced longitudinal depressions (Fig. 5); the disk of the male pronotum is without granulations, appearing smooth even under magnification, except for weak roughening anterolaterally; the elytra and most or nearly all of the pronotum are dull black, not shining; or, if a shining red color present (*pyrois*), it is restricted to the pronotum.

The Guerrero specimen, which is a large male, differs from those collected in Temascaltepec by the lack of an anterior pronotal tooth, by being less distinctly granulate and darker, less shining green. It is interesting that *halffterorum* is evidently more widely distributed geographically than the special ecological conditions of Temascaltepec might lead one to predict. I do not know the Guerrero locality, but the elevation (2400 ft, 735 m) suggests a significantly different ecological setting from that of the environs of Temascaltepec. The ecological comments below are based on observations made in the Temascaltepec area.

Temascaltepec is located on the southern slopes of the Transverse Volcanic Range at 19°02′N, 100°02′W. The area supports extensive stands of oak-pine to pine-oak forests on very uneven terrain. All specimens collected there have come from inside or near the margins of the forests between 1935 and 2360 m (6350 and 7750 ft). As was originally reported by Hinton (1935) and later by Halffter and Matthews (1966), who referred to this species as *endymion, P. halffterorum* is mycetophagous and attracted only to several species of wild mushrooms (none yet identified) common during the rainy season. It has never been found associated with excrement of the many domestic animals (cattle, horses, burros, swine) which roam the area nor in

human excrement or carrion used to bait pitfall traps. When partially decomposed, mushrooms are treated by adults as is excrement or carrion by other *Phanaeus*: beginning with the stalk, the fungus is packed by pieces into the blind end of a tunnel dug directly beneath it. Here it is either consumed by the adults or used to fashion brood balls.

Mycetophagy by scarabaeine dung beetles has been known for many years. While many species have been collected from decomposing fungi (see Halffter and Matthews, 1966), very few appear to be as strictly mycetophagous as is *halffterorum*. The following have also been collected from wild mushrooms in the Temascaltepec area, although only the former is evidently strictly mycetophagous: *Oniticellus rhinocerulus* Bates; *Phanaeus daphnis* Harold (Hinton, 1935), otherwise very common in cattle dung; one species each (not yet identified) of *Ateuchus* and *Onthophagus* which are more commonly collected in cattle and horse dung.

The southern slopes of the Transverse Volcanic Range are interrupted by a series of valley systems which descend steeply to the valley of the Balsas River. Temascaltepec is located near the upper (northern) end of one such valley system. Of zoogeographic interest is the fact that Temascaltepec, like similar places along the Transverse Volcanic Range, supports a dung beetle fauna which comprises both nearctic and neotropical elements. *Copris, Onthophagus, Oniticellus* and *Ceratoptrupes* (Geotrupinae) are northern contributions; *Phanaeus, Ateuchus, Canthidium, Deltochilum, Dichotomius* and *Coprophanaeus* are southern representatives. Such faunal mixing in the Mexican transition zone has been discussed by Halffter (1964, 1976). In accordance with ideas I presented in 1972, *P. halffterorum* can be interpreted as the product of relatively recent speciation; it undoubtedly represents the deepest northward eco-geographic penetration of the *P. splendidulus*-group into North America.

P. halffterorum has been successfully reared in the laboratory. Two pairs of field-collected adults were introduced into the same vertical terrarium (95 × 60 × 7 cm) on 12 July, 1976, and provided decomposing fungi from the type locality. Later, partially decomposed commercial (edible) mushrooms were provided to replace the original food supply, which was buried quickly. Four brood balls were recovered on 14 September; all nesting details agreed with those of other known *Phanaeus* (Halffter and Matthews, 1966; Halffter, 1977). A fifth brood ball was recovered on October 6, at which time surviving adults (1 male, 2 females) were supplied with human excrement. A sixth brood ball, provisioned with human excrement, was recovered on 8 November; it yielded an egg in early stages of decomposition. Although field and laboratory data may suggest strict mycetophagy, further rearing trials with excrement are necessary before concluding whether or not *halffterorum* requires fungi for successful nidification. All five

fungus-provisioned brood balls yielded eggs which were allowed to develop to 3rd (final) instar larvae. The larva of *halffterorum* is virtually identical to those of other known phanaeines (Edmonds and Halffter, 1978).

Acknowledgments

This paper reports partial results of a cooperative project on dung beetle ecology supported jointly by the National Science Foundation (U.S.–Mexico Cooperative Science Program, Grant No. INT76-06712) and the Consejo Nacional de Ciencia y Tecnología (Programa Nacional Indicativo de Ecología—Proyecto "Interacciones entre ganado y pastizales"). Mr. Michael Thompson prepared the photographs; Mr. James McCabe prepared the drawings.

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Footnotes

[1] This specimen is evidently one of the series of eleven referred to by Hinton, 1935. I have been unable to locate the remaining ten specimens.

[2] Terminology used here is that established by Edmonds, 1972.

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A NEW SUBSPECIES OF *POLIAENUS NUEVOLEONIS* CHEMSAK AND LINSLEY FROM SOUTHERN ARIZONA (COLEOPTERA: CERAMBYCIDAE)

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In a recent review of Mexican Pogonocherini, Chemsak and Linsley (1975) described the new species *Poliaenus nuevoleonis* from a male taken in northeastern Mexico near Monterrey, Nuevo Leon. Subsequently, I have examined over 70 specimens of that species from the mountains of western Texas and southeastern Arizona, as well as a single specimen from western Mexico about 100 km west of the city of Durango. The specimens from Arizona and western Mexico are readily distinguished from those from Texas and northeastern Mexico and merit subspecific recognition. Below I have modified the original description of *P. nuevoleonis* to accommodate the substantial morphological variation exhibited by the species.

Poliaenus nuevoleonis Chemsak and Linsley

Male.—Form elongate-robust, sides subparallel. Integument shining, red-brown to blackish, clothed throughout with fine, appressed, moderately dense pubescence partially obscuring surface, less densely clothed with long flying hairs which are predominantly dark brown or black on dorsum, white on venter, intermixed on appendages. Head with pubescence brownish white, vaguely washed with gold on occiput; frons two-thirds again as broad as high; eye with lower lobe subquadrate, slightly erect, upper lobe distinctly narrower than interocular space; antenna red-brown, exceeding elytral apex by three or four segments, scape moderately slender, attaining lateral prothoracic tubercle, third segment longest, fourth subequal to scape, half again as long as fifth, fourth to eleventh basally annulate with dense, appressed, white pubescence. Pronotum with pubescence brownish white, distinctly washed with golden-orange on basal half; width across lateral tubercles one and one-fifth to one and one-third times length, dorsal tubercles moderate, distinctly separated by flat pronotal disc, lateral tubercles moderate to rather prominent, blunt, occasionally slightly recurved. Elytra two times as long as wide, with a V-shaped antemedian impression extending from suture to humeri, apices conjointly or separately rounded; lateral and median costae fine, subdued or moderately prominent, extending from humeri to apical third or fourth of elytra, thence becoming evanescent and

indicated only by a few minute dark brown penicilli; subsutural costa indistinct, indicated only by a prominently penicillate sub-basal gibbosity and by an elongate post median swelling containing from one to five prominent, separate or confluent penicilli; punctures coarse, separate basally and laterally, becoming shallower apically, vanishing abruptly at apical third; pubescence moderate to dense, often largely obscuring basal punctures, brownish white, washed with gold along subsutural costae, subsutural penicilli dark brown, occasionally margined with orange. Abdominal sternites densely fringed with white hairs, fifth subequal to fourth, apex broadly rounded or subtruncate. Length 5.9–10.2 mm.

Female.—Form slightly more robust, antennae slightly shorter than in male. Upper lobe of eye about half as wide as interocular space. Fifth abdominal sternite about twice as long as fourth, distinctly impressed medially, apex broadly rounded to subtruncate. Length 6.1–10.9 mm.

Two subspecies, widely separated geographically, can be recognized.

Poliaenus nuevoleonis nuevoleonis Chemsak and Linsley

Lateral and median elytral costae fairly prominent. Pubescence sufficiently dense to largely obscure basal elytral punctures and give dorsum a hoary appearance. Appressed white pubescence covering at least basal three-fifths of antennal segments four to ten. Length 7.4–10.2 mm.

Material examined.—MEXICO: NUEVO LEON: Holotype ♂ from Chipinque Mesa, 5400 ft near Monterrey, VII-23-63 (H. Howden); Monterrey, 1 ♀, III-17-53. COAHUILA: Cuesta La Murrala, 1 ♂, IX-12-76 (J. A. Chemsak, J. Powell, A. and M. Michelbacher). TEXAS: Big Bend National Park, Chisos Mts., Brewster Co.: 1 ♂, VII-4 to 6-61 (R. L. Westcott); 4 ♂ ♂, 2 ♀ ♀, VII-16 to 17-73 (F. T. Hovore, beaten ex *Quercus*). Davis Mountain State Park, Jeff Davis Co.: 1 ♀, VII-18 to 21-73 (F. T. Hovore, at light).

Poliaenus nuevoleonis similnegundo, new subspecies

Elytral costae usually subdued. Pubescence not obscuring basal elytral punctures, integument sufficiently visible to give dorsum a dark brown appearance. Appressed white pubescence covering at most basal half of antennal segments four to ten. Length 6.1–10.9 mm.

Known habitat, range, and flight period.—Oak woodland of southern Arizona (May to September) and Durango, Mexico (July).

Material examined.—Holotype female (California Academy of Sciences Type #13247) from Santa Rita Lodge, elevation 4960 feet, VII-14-75, Madera Canyon, Santa Cruz Co., Arizona (D. D. Skiles at light); allotype (CAS), VII-4-72, Madera Canyon, Santa Cruz Co., Arizona (D. G. Marqua). Paratypes. ARIZONA. Pima Co.: Kitt Peak, 6000 feet, Baboquivari Mts., 1 ♀, VIII-9-78 (D. Skiles, at light); Sabino Canyon, 1 ♂, IX-4-61 (J. S.

Buckett). Cochise Co.: Miller Canyon, Huachuca Mts., 1 ♂, VII-18-71 (D. G. Marqua), 1 ♂, VII-12-75 (E. F. Giesbert); Carr Canyon, Huachuca Mts., 1 ♀, IX-4-59 (R. L. Westcott); Cave Canyon, Huachuca Mts., 1 ♀, VIII-6-78 (D. Skiles, beaten ex dead *Quercus hypoleucoides*); Cochise Stronghold, Dragoon Mts., 1 ♀, VII-12-77 (D. Skiles at light), Cave Creek Ranch, Chiricahua Mts., 1 ♂, VIII-19-65 (G. W. Forister, at light); 5 mi W Portal, Chiricahua Mts., 1 ♂, VIII-14-58 (G. G. Moore). Santa Cruz Co.: Santa Rita Mountains, 6000 feet, 1 ♂, IX-15-33 (Bryant, Lot 238; labeled "*Poliaenus negundo* (Schaeffer)/Det. Knull '56"; also labeled "*Pogonocherus arizonicus* Schaeffer"). Madera Canyon, Santa Rita Mountains, 1 ♂, IX-4-66, 1 ♂, 1 ♀, IX-5-66 (M. E. Pendleton): 2 ♂♂, VIII-16-67 (C. D. Johnson, at light); 1 ♂, 1 ♀, IX-3 to 5-69 (J. Powell, at light); 1 ♀, VII-23 to 25-58, 1 ♀, IX-2-59 (R. L. Westcott); 1 ♀, IX-3-64 (G. H. Nelson, at light); 1 ♀, IX-5-59 (L. M. Martin, at light); 1 ♀, V-22-63 (J. G. Franclemont, 4880 feet); 1 ♀, IX-4-67 (A. S. Menke, 4880 feet); 1 ♂, IX-29-63 (V. L. Westerby, 4880 feet); 1 ♀, VII-1-63, 1 ♂, VII-2-63, 1 ♀, VII-5-63 (J. D. Marshall, 4880 feet); 1 ♀, VIII-6-69, 1 ♀, VIII-71, 1 ♀, VIII-28-71 (E. F. Giesbert, at light); 3 ♂♂, VII-23 to 24-71, 1 ♂, VIII-28-71, 2 ♀♀, VIII-8-77, 2 ♂♂, 1 ♀, VII-12-78 (F. T. Hovore at light); 1 ♂, 1 ♀, VII-27-76 (F. T. Hovore, beaten together ex dead *Quercus*). 1 ♀, VII-23-74, 1 ♀, VII-9-75, 1 ♀, VII-14-75, 1 ♂, IX-12-75, 1 ♂, IX-20-75, 1 ♀, VII-10-77, 1 ♂, VII-12-77 (D. Skiles, at light and beaten ex dead *Quercus*); 17 ♀♀, VII-7, 9, 19, 29-71, IX-7-71, VII-11, 12, 18-72, VIII-4, 8-72, VII-21-73, VII-20-74, VII-15-75, VIII-15-75, 6 ♂♂, VII-18, 19, 28-71, IX-7-71, VII-14-75, VIII-15-75 (D. G. Marqua, at light).

Also assignable to this subspecies but not included as paratypes: 1 ♂, Huachuca Mts., Arizona (Van Dyke collection); 1 ♂, 3 mi E El Salto, Durango, Mexico, VII-3-64 (L. A. Kelton).

Diagnosis.—The fact that *P. nuevoleonis*, though rather common, remained undescribed until recently is undoubtedly due to its remarkable resemblance to *P. negundo* (Schaeffer) and to the fact that both species are frequently taken together at light in oak woodlands throughout southeastern Arizona.

Presumably, these congeners are able to coexist by utilizing different hosts. *Poliaenus negundo* is known to attack sumac and box elder (Linsley, 1935), and *P. nuevoleonis* probably attacks various species of oak, since a small number of specimens have been beaten from dead, leaved branches of *Quercus* sp. in the Davis and Chisos Mountains of Texas (F. T. Hovore, E. F. Giesbert) and from dead, leaved branches of *Q. hypoleucoides* A. Camus in the Santa Rita and Huachuca Mountains of southern Arizona (F. T. Hovore, D. Skiles). Beyer (1908) reported that four specimens of *P. negundo* from Arizona's Huachuca Mountains emerged in 1907 from oak twigs girdled in 1905 by *Oncideres quercus* Skinner. However, as I am

unaware of any other records of *P. negundo* from oak, I am inclined to believe that Beyer in fact reared *P. nuevoleonis*.

Poliaenus nuevoleonis and *P. negundo* can usually be distinguished with the unaided eye by the different color patterns of the elytral pubescence. In the former the pattern is very faint and the elytra appear rather uniformly brown with a slight hoary wash. In *negundo* the dark brown base of the elytra contrasts sharply with the dense, yellowish-brown pubescence of the antemedian V-shaped impression. Despite this difference, specimens of *P. nuevoleonis* are easily mistaken for slightly rubbed specimens of *P. negundo*.

Under the microscope the two species are readily distinguished by the distinct structures of the pronotal disc. In *nuevoleonis* the discal tubercles can best be described as circular cones arising from a flat pronotal disc; in *negundo* the discal tubercles are little more than the lateral limits of a discal pronotal gibbosity. In addition, the flying hairs on the dorsal surface of the posterior tarsi are brown intermixed with white in *nuevoleonis,* whereas they are almost invariably entirely white in *negundo,* though they may appear dark when illuminated from certain angles.

From the long series of *P. nuevoleonis* I have examined, it is apparent that *P. nuevoleonis, P. sparsus* Chemsak and Linsley, and *P. batesi* Linsley are closely related and may even be conspecific. However, the latter two species are known only from single specimens so that a definitive analysis of the specific status of each must await the collection of further material. I have examined the type of *P. sparsus* (California Academy of Sciences) and a 35 mm color slide of the type of *P. batesi* (courtesy E. G. Linsley and J. A. Chemsak) and offer the following observations.

The structural similarities between the diminutive type of *P. sparsus* and smaller specimens of *P. nuevoleonis similnegundo* leave me with the impression that the two species may ultimately prove to be one. Nevertheless, when compared side by side with a series of small *P. nuevoleonis similnegundo,* the specimen of *P. sparsus* immediately stands apart as having rather testaceous integument rather densely covered with golden pubescence, as opposed to dark brown integument rather sparsely covered with grey pubescence. In addition, *P. sparsus* is slightly smaller than the smallest paratypical *P. nuevoleonis similnegundo,* and the basal elytral punctures of the former are distinctly coarser. Hence the two species cannot be synonymized on the basis of the available material.

On the other hand, I find it difficult to believe that *P. nuevoleonis* and *P. batesi* are specifically distinct. Specimens of *nuevoleonis,* particularly densely pubescent ones such as those I have seen from the Chisos Mountains of Texas, key to *batesi* in Linsley's (1935) key to the genus. In addition, although I have seen only a slide of the unique specimen of *batesi* from central Guatemala, the slide clearly shows all diagnostic characters,

and the specimen differs from large, densely pubescent specimens of *nuevoleonis* only in the more prominent and dramatically orange penicilli of the subsutural elytral costae. However, the subsutural penicilli of *nuevoleonis,* while appearing dark brown or black to the naked eye, are in fact often margined with orange. This is particularly true of the postmedian penicilli. Hence the orange penicilli of *batesi,* which under the microscope are seen to have dark brown centers at the base of the elytra and a few dark brown hairs on the apical third of the elytra, merely appear to be extreme versions of a color tendency apparent in *nuevoleonis.*

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GENETIC CONFIRMATION OF THE SPECIFIC STATUS OF THE *SPEYERIA ADIASTE* GROUP IN CALIFORNIA (LEPIDOPTERA: NYMPHALIDAE)

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The *Speyeria adiaste* Edwards group is composed of three closely related subspecies occurring in suitable habitats in the Coast Ranges and extreme southern Sierra Nevada of California. These subspecies are well illustrated on Plate 24 in The Butterflies of North America (Howe, 1975). *Speyeria adiaste* was described by W. H. Edwards (1864) and the type locality was fixed by DosPassos and Grey (1947) as the Santa Cruz Mountains, California, where existing populations of *S. adiaste adiaste,* the northernmost and darkest member of the group, occur. *Speyeria adiaste clemencei* (Comstock) has a lighter fulvous ground color and less pronounced dark markings on the upper wing surface than the nominate species (Comstock, 1925). It occurs in the Coast Ranges from Monterey Co. to near the town of San Luis Obispo. The now extinct *S. adiaste atossa* (Edwards) was recorded in the Tehachapi and Tejon Mountains and in the Mt. Pinos region. In overall appearance it resembled its northern counterparts except for a clear yellow-brown ground color and further reduction of the upper surface markings.

These three geographically disjunct subspecies form a color cline ranging from the dark northern *S. adiaste adiaste* to the pale southern *S. adiaste atossa.* Although not yet determined for the *adiaste* group, several other subspecies groups in the genus *Speyeria* (*callippe, coronis, zerene*) display extremely close genetic similarity despite evident phenotypic change (Brittnacher et al., 1978). It is likely that the *adiaste* group fits into this pattern which suggests a rather recent evolutionary divergence of the different color forms.

The distributional limits of these subspecies seem, in part, to be determined by the availability of their violet (*Viola*) food plants and by desiccation tolerances of first instar larvae to dry diapause period (summer–fall) conditions (Sims, unpublished data). Xeric conditions tend to limit distributions of many violet species and prove fatal to species lacking adequate desiccation resistance. *Speyeria adiaste* may once have occurred in an unbroken range throughout the coastal mountains. Division of the range was

possibly influenced by the drier climatic conditions of the Pliocene (Axelrod, 1948) or the pluvial periods of the Pleistocene. The warmer and drier post-Pleistocene conditions would have supplemented the process of range limitation.

Since the original description, the taxonomic status of *S. adiaste adiaste* and the later named subspecies has been in doubt. The most recent systematic treatment of the genus *Speyeria* (DosPassos and Grey, 1947) regards the *adiaste* complex as a subspecies of *S. egleis* (Behr). Although *S. egleis* exhibits a much wider distribution than *S. adiaste,* the groups are (or were) completely allopatric except in the Tehachapi Mountains. In this latter location, the species populations were spatially isolated by elevation, *S. egleis* preferring the higher peaks and slopes while *S. adiaste atossa* frequented mid-elevation habitats. Other interspecific barriers to reproduction might well have included differences in species specific pheromones or mating behavior (Magnus, 1958).

Phenotypically, specimens within populations of the three taxa in the *adiaste* group are quite uniform in contrast to many other species in the genus (Moeck, 1957). *Speyeria egleis* often exhibits remarkable intrapopulation variation both in coloration of the disc (basal undersurface of hind wing) and in the silvering or absence of silvering of the hind wing spots.

The taxonomic relationship of *S. adiaste* has recently undergone another shuffling in which the group regained specific status (Emmel and Emmel, 1973; Howe, 1975). The purpose of this paper is to present genetic evidence which ex post facto justifies this latest separation of the *S. adiaste* group.

Genetic Differentiation

Gel electrophoretic techniques are well known and currently widely used to study inter- and intraspecific levels of genetic variability in diverse groups of organisms. Techniques of gel electrophoresis and enzyme assay allow identification of allelic variation at single gene loci. When data are obtained from a "moderate" number of enzyme loci, the results, with certain assumptions, may be extrapolated to the genome as a whole. The loci studied are assumed to represent a random sample of the genome with respect to allelic variation. Possible sources of bias in such an assumption have been cited by Lewontin and Hubby (1966) and Ayala et al. (1970). It has been amply demonstrated that gel electrophoresis is an extremely valuable systematic tool (see Avise (1974) for review). Ayala (1973) and Ayala and Dobzhansky (1974) have used allozyme data as diagnostic characters for subspecies of *Drosophila willistoni* and *D. pseudoobscura.*

We examined genetic variation at 16 loci in all ten species of *Speyeria* occurring in California plus several of the subspecies existing in the *callippe, coronis, hydaspe,* and *zerene* groups (Brittnacher et al., 1978). With few

Table 1. Genetic similarity (above diagonal) and genetic distance (below diagonal) for seven species in the genus *Speyeria*.

	1	2	3	4	5	6	7
1. *adiaste*		.775	.866	.798	.852	.917	.762
2. *atlantis*	.255		.913	.954	.950	.801	.922
3. *callippe*	.144	.091		.933	.985	.881	.901
4. *coronis*	.225	.047	.069		.938	.883	.903
5. *egleis*	.161	.051	.015	.064		.872	.938
6. *hydaspe*	.087	.222	.126	.125	.138		.790
7. *zerene*	.272	.081	.104	.102	.064	.236	

exceptions, only males were used in the assays. Females were used in a companion study of the reproductive biology of the genus.

Populations of *S. egleis egleis* from the following Sierra Nevada locations were analyzed: Bowman Lake, Nevada Co., el. 1700 m (n = 8); Donner Pass, Placer Co., el. 2100 m (n = 5); and Yuba Pass, Sierra Co., el. 2000 m (n = 10). Two populations of *S. adiaste clemencei* were sampled: Arroyo Seco Camp, el. 260 m (n = 19) and Chew's Ridge, el. 1100–1500 m (n = 45), both in the coast range of Monterey Co. California.

Speyeria adiaste clemencei and *S. egleis egleis* were found to have two fixed differences at the sixteen loci studied. These were for glyceraldehyde-3-phosphate dehydrogenase and glucose-6-phosphate dehydrogenase (see Brittnacher et al., 1978, for details).

The amount of genetic differentiation between *S. adiaste* and *S. egleis* is substantial when compared to the genetic differentiation between other species of *Speyeria*. Table 1 summarizes the differentiation found in *Speyeria* using Nei's (1972) method of calculating genetic distance, *D*, and genetic identity, *I*. It can be seen that the genetic distance between *S. egleis* and *S. adiaste* is greater than the distance between *S. egleis* and *S. atlantis*, *S. callippe*, *S. coronis*, and *S. zerene*. It is thus unlikely, based on this genetic evidence alone, that the members of the *S. adiaste* group are subspecies of *S. egleis*.

Karyotype Determination

Chromosome numbers of *S. adiaste clemencei* and *S. egleis egleis* were determined in view of the potential for additional substantiation of the allelic differences. Chromosome counts were made in 19 nuclei in testes of 6 *S. adiaste clemencei* males field collected at Chew's Ridge on June 11, 1974. Counts were similarly made in 10 nuclei in testes of 3 *S. egleis egleis* pupae derived from the population at Loon Lake, El Dorado Co., California.

Cytological techniques followed for *S. adiaste clemencei* involved fixa-

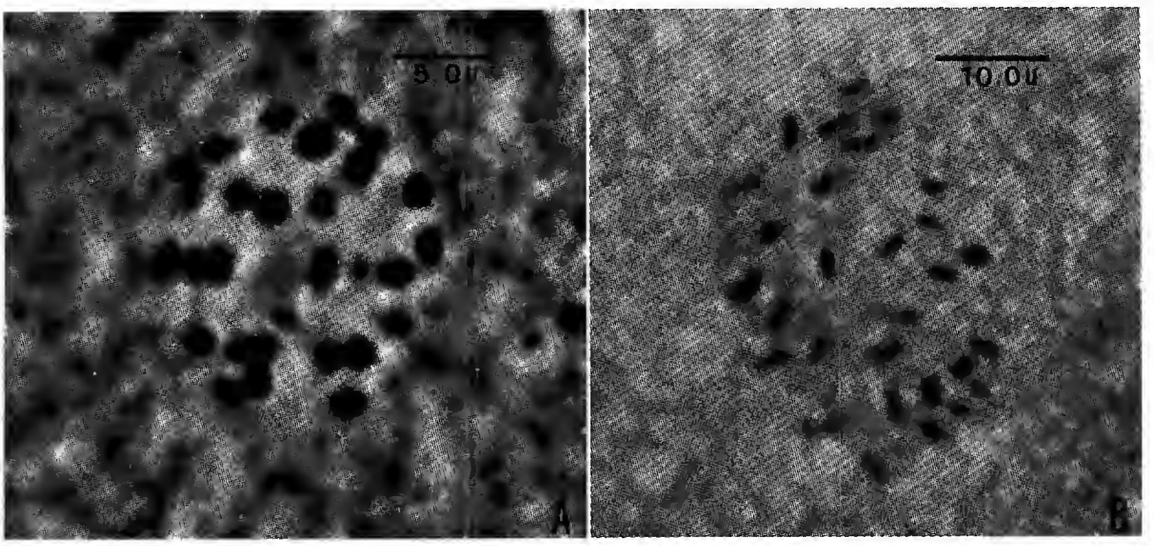

Fig. 1. Chromosomes of *Speyeria*, (A) *S. adiaste clemencei*, N = 29, metaphase; (B) *S. egleis egleis*, N = 29, metaphase.

tion for 5 minutes in a 3:1 absolute ethanol:glacial acetic acid solution, staining with 0.5% lacto-acetoorcein, and squashing on a slide using hand pressure (Emmel, 1968). A modified squash-air dry technique described by Goodpasture (1976) was used for chromosome counts of *S. egleis egleis*. Preparations were examined under oil using phase contrast illumination at a magnification of 960×. Photographs were taken on Kodak High Contrast Copy 35 mm film at a film plane magnification of 400×.

In all sufficiently clear preparations, the haploid number (N) was found to be 29 for both *S. adiaste* and *S. egleis* (Fig. 1). This count is identical to the majority of previously determined species in the genus (Maeki and Remington, 1960). Exceptions occur in the *S. callippe* and *S. coronis* groups where apparently N = 30. Curiously, *S. callippe* and *S. egleis* are cytologically distinct despite having the highest genetic similarity value (.985) of all species studied.

Immature Stages

Little other comparative biological data is available on the *S. adiaste* and *S. egleis* groups. Edwards (1897) described and illustrated the life history of *S. egleis* from Colorado. Comstock and Dammers (1931) described the mature larva and pupa of *S. adiaste atossa* from Lebec, Kern Co., California. Adequate distinguishing characters cannot be determined from the descriptions except for the slightly larger mature size of the *S. adiaste atossa* larva (35 mm vs. approx. 31 mm for *S. egleis*) which may simply be a sex-related difference. We believe it significant to note that mature larvae of both are characterized by an irregular yellowish patch on the dorsum of the head capsule, a trait missing in California *S. callippe* and *S. coronis*.

Summary

Speyeria adiaste clemencei, long considered a member of the *S. egleis* group, shows a relatively low degree of genetic similarity (I = .852) to this species. Two fixed differences were present among sixteen loci studied. From a perspective of genetic relationships in other *Speyeria* this divergence appears significant at the species level. The marked phenotypic distinctiveness of the *Speyeria adiaste* group, uniformity of phenotype within populations, geographic isolation, and lack of hybridization are additional factors arguing for recognition of specific distinction. The chromosome number (N = 29) of both *S. adiaste* and *S. egleis* is similar to the majority of other *Speyeria* and does not provide an adequate index of relationship. Both groups have similar immature stages with only minor color differences. In these two species, it appears that allozyme characters are better differentiated than chromosome number or immature stage morphology.

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EMIGRATION RESPONSE BEHAVIOR: II: THE RESPONSES OF *DROSOPHILA BUSCKII* (DIPTERA: DROSOPHILIDAE)[1]

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The movement of members of a population from one geographic locality to another is an important factor in the evolutionary process. It is clear that not all members of a given population emigrate. Of those members which do move, some are compelled by genetic factors, some by environmental factors and some by the interaction of both. While emigrants must be capable of surviving and reproducing in the new localities, fine level adaptations to a new area evolve only *after* arrival. Thus, the possibility of extending the range of a species depends on the ability of the genetic architecture of the emigrants to respond to a new environment in addition to their propensity to move from an old one. It follows that the examination of genetic and environmental factors influencing movement from one locality to another is of prime importance to evolutionary and behavioral biology.

This is a report from an ongoing study that is examining the *interacting effects of genotypes and environments* on the movement of *Drosophila* from their place of origin to new locations. The active change in location of members of a population results from two distinguishable processes, namely, migration and dispersal. While these terms have had various meanings, Rockwell et al. (1978) encouraged the use of the following definitions: *Migration*—the goal oriented movement of a fraction of the population; *Dispersal*—the movement of a fraction of a population as a result of the general (random) activity of its members. The overall movement of organisms from their place of origin to a new location is termed *emigration response behavior.*

Emigration response behavior of *Drosophila* has been examined in the laboratory by a number of researchers who have used a system devised by Sakai et al. (1958). That system consists of a set of four interconnected vials through which individual flies can move (Fig. 1). Emigration response behavior is measured as the number (or percentage) of individuals leaving the central vial. Rockwell et al. (1978) pointed out that this single measurement of emigration response confounds migration and dispersal. They proposed that by measuring emigration responses in the Sakai system relative to four specific environmental configurations, one could obtain a clearer view of the relative contributions of migration and dispersal to the overall emigration response behavior of a species (or strain).

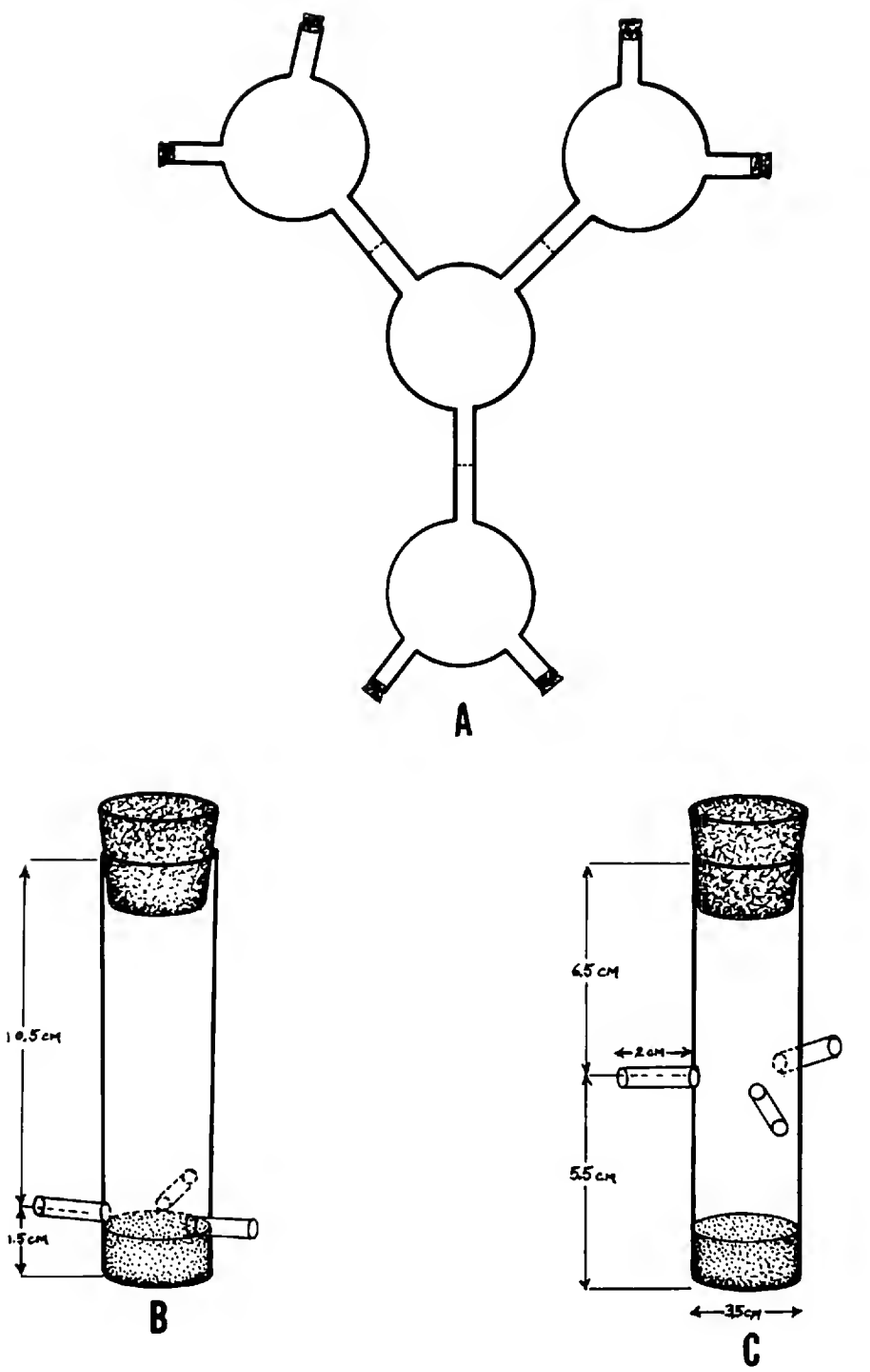

Fig. 1. The emigration response behavior apparatus modeled after Sakai et al. (1958). A—the arrangement of vials; B—low vial; C—high vial.

The specific environmental configurations are the four possible combinations of two levels of each of two factors, namely *height* of the connecting tubes and *lighting condition*. The original Sakai system utilizes connecting tubes which are about 4 cm above the level of the food surface in the vials (Fig. 1C). As such, passage from the central vial to the three peripheral vials can be viewed as three-dimensional; that is, requiring movement through a volume. The use of vials whose connecting tubes are at the same level as the food surface changes this to two-dimensional movement involving only

area. If the passage of flies through this system contains a general activity component, one would expect substantially more emigration in the vials with the low connecting tubes simply because the flies would have more chance, in a fixed time period, to encounter the connecting tubes. Thus, the greater the difference between the emigration responses measured in the two types of vials (high versus low), the greater is the dispersal component of the overall emigration response behavior.

The role of light as a stimulus that increases general activity in *Drosophila* has been extensively noted (Grossfield, 1971). If light plays this role in the Sakai system and if the passage of flies through this system contains a general activity component, one would expect substantially more emigration in the light than in the dark. Thus, the greater the difference between the emigration responses measured in the light versus dark, the greater the dispersal component of the overall emigration response behavior.

The present paper focuses on the emigration response behavior of *Drosophila busckii.* This species, like *D. melanogaster* has a global distribution. However, there is a phylogenetic peculiarity of the genus in that it is the only member of its subgenus *dorsilopha* (Throckmorton, 1975). In addition, *D. busckii* possesses an inordinately low level of genic variation (and, hence, heterozygosity) which contrasts it not only with the rest of the genus but with many other organisms (Prakash, 1973). The inclusion of this species in the overall study of the interacting effects of genotype and environment on the movement of *Drosophila* from one locality to another is especially important for two reasons. First, because of the taxonomic and genetic distinctness of this species in the genus, the evaluation of its emigration response behavior will provide information on the general applicability of this experimental system, and the conclusions reached using it, to studies of interlocality movement in the genus.

Second, because of the low heterozygosity of *D. busckii,* the extent to which the emigration response changes across the four environmental configurations will provide important information on the general relationship between behavioral plasticity (i.e., flexibility) and genetic architecture. While it is widely held that the level of plasticity of a given behavioral trait is related to underlying genetic architecture such as the level of heterozygosity (Dobzhansky, 1973), most studies on the nature of that relationship have only used species that are quite heterozygous in nature (Caspari, 1967; Rockwell et al., 1975).

Methods and Materials

Stocks and Culturing

The strain of *Drosophila busckii* used in these experiments was collected at Wyeth Farm, Glenburnie, Ontario, in the fall of 1975. Since that time, it

has been maintained as a mass culture in ½ pint bottles on a medium composed of equal volumes of instant mashed potatoes and water (Tegosept® is added to reduce mold contamination). The stock is maintained at 20.0°C, 85% relative humidity and constant illumination.

Equipment

The migration vials are modeled after those of Sakai et al. (1958) and are depicted in Figure 1. Two types of vials were used:

a) *high vials* (Fig. 1C) in which the connecting tubes are 4.0 cm above the surface of the medium;
b) *low vials* (Fig. 1B) in which the connecting tubes are at the same level as the surface of the medium.

As depicted in Figure 1A, four high vials or four low vials were connected with clear tape to form a single migration system. The unused connecting tubes of the three peripheral vials were plugged with corks. A mixture of instant mashed potatoes and water (1:1) was used as the medium. The systems were assembled one hour before the beginning of experimental trials. Each assembled system was placed in an open plastic tray measuring 28 × 28 × 16 cm high. The inside of each of these trays had been painted white and the outside had been painted black. The painting of the trays served to eliminate extraneous visual cues and to provide diffuse uniform illumination. The trays containing the migration systems were placed in a 20.0°C environmental chamber.

Procedure

Flies were collected daily from replicate culture bottles and batches of 20 males and 20 females were placed together in 8 dram food vials. These were stored in an incubator at 20.0°C, 85% relative humidity and constant illumination. A set of 50 males between 7 and 10 days old was randomly collected from these vials and placed in an empty 8 dram vial for 30 minutes. Humidified CO_2 was used as the anesthesia for these procedures.

A given set of 50 males was aspirated into the central vial of either a high or a low migration system. If the system was to be tested in the dark, the tray containing the system (and the flies) was immediately covered with black cloth. Preliminary studies demonstrated that no light entered such trays. If the system was to be tested in the light, the tray containing the system was placed beneath a fluorescent light fixture (consisting of two 40 watt tubes suspended 24 inches above the tray).

After inserting the flies and placing the trays in the appropriate lighting condition, the system was left undisturbed for 24 hours (until 1000 hours on the following day). At that time, the number of flies in the three peripheral

vials was determined. The total number of flies in the three peripheral vials was used as the measure of *emigration response* for a given configuration. The measure can range from 0 to 50.

Experimental Design and Statistical Procedures

In order to examine the relationship between height and lighting condition, the experiments were performed in a factorial fashion. Three replicates of each combination of the levels of the two factors were performed in a randomized blocks fashion. Preliminary analysis of the data demonstrated no effects of blocks, so the replicate sources of variation were pooled (Winer, 1971). The data were then analyzed with factorial analysis of variance. The factorial design and analysis were used to assess whether the factors affect the emigration response behavior and to determine whether the two factors interact.

The emigration responses of *D. busckii* were compared to those of *D. melanogaster* with factorial analysis of variance. The emigration responses of *D. melanogaster* used in that comparison were measured under conditions identical to those just described and formed a part of a study reported in Rockwell et al. (1978).

Results

The emigration responses of male *D. busckii* in the four environmental configurations are given in Table 1 as means with their associated standard errors. The responses were analyzed with factorial analysis of variance and the results of that analysis are summarized in Table 2. There is a highly significant effect of tube height overall; the emigration response is greater in the low tubes. There is no significant effect of lighting condition on the emigration response. Importantly, there is no significant interaction between tube height and lighting condition; tube height modulates the response equivalently in both the light and the dark.

The emigration responses of *D. busckii* were compared to those of *D.*

Table 1. The emigration response behavior of male *Drosophila busckii* measured in the four conditions of the Sakai system.

Lighting condition	Tube height	
	Low	High
Constant light	31.33 ± 1.76	20.33 ± 2.33
Constant dark	36.33 ± 4.70	19.33 ± 2.84

NB: ±Standard errors.

Table 2. Analysis of variance of the emigration response behavior of male *Drosophila busckii*.

Source of variation	Degrees of freedom	Mean square
Tube height (H)	1	588.00[2]
Lighting condition (L)	1	12.00
H × L	1	27.00
Error	8	29.08

NB: All sources were tested over the error term.
[2] Significant at the 0.01 level of probability.

melanogaster using the three factor analysis of variance summarized in Table 3. Examining the main effects first, it is clear that there is no *overall* difference between the two species. That is, the emigration response behaviors of the two species, *averaged across the four environmental configurations,* do not differ significantly. In sharp contrast, the overall emigration responses for the two tube heights, averaged across lighting conditions and species, are quite significantly different. The emigration response in the low tubes is twice that in the high tubes (34.15 versus 16.99). The overall emigration responses for the two lighting conditions, averaged across tube height and species, are significantly different. The emigration response in the dark is greater than that in the light (28.57 versus 22.57).

Of crucial importance is the highly significant three-way interaction between tube height, lighting condition and species. Given the simultaneous

Table 3. Analysis of variance of the emigration response behavior of male *Drosophila busckii* and *D. melanogaster*.

Source of variation	Degrees of freedom	Mean square
Tube height (H)	1	1768.17[2]
Lighting condition (L)	1	216.00[3]
Species (S)	1	37.50
H × L	1	216.00[3]
H × S	1	60.16
L × S	1	96.00
H × L × S	1	486.00[2]
Error	16	44.99

NB: All sources were tested over the error term.
[2] Significant at the 0.01 level of probability.
[3] Significant at the 0.05 level of probability.

occurrence of a significant interaction between tube height and lighting condition and the lack of any significant interaction between tube height and species, the three-way interaction may reasonably be interpreted as a nonadditive effect between the two species for the tube height by lighting condition interaction. That is, the interrelationship between tube height and lighting condition, in their joint effect on emigration response, differs between the two species.

This interpretation is further supported by comparing the separate analyses of tube height and lighting condition effects for the two species. In the factorial analysis of tube height and lighting condition effects on the emigration response behavior of male *D. melanogaster* (Rockwell et al., 1978), it was shown that the tube height by lighting condition interaction is highly significant. For *D. melanogaster,* then, the effects of tube height and lighting condition are not independent; tube height modulates the response differentially with light. Recalling the analysis summarized in Table 2, tube height modulates the emigration response of *D. busckii* equivalently in the light and in the dark. Thus, the interdependence of tube height and lighting condition on the emigration response behavior of these two species is different.

Discussion and Conclusions

It is clear that tube height modulates the emigration response behavior of *Drosophila busckii.* The greater emigration response displayed in the low tubes is consistent with the existence of a general activity component in the overall emigration response behavior of this species. As explained earlier, such a component would be expected to result in more two-dimensional movement than three-dimensional movement.

There is no apparent effect of lighting condition on the emigration response behavior of this species; the emigration response is the same in constant light and constant dark. This result is not in agreement with the accentuating effect of light on general activity widely noted for *Drosophila* (Carpenter, 1905; Manning, 1965). This difference may reflect a peculiarity of the overall general activity behavior of *D. busckii.* It may also reflect the existence of several general activity programs in this species, each of which may serve as a component of different overall behavior systems. While the latter explanation is consistent with the results of experiments with *D. melanogaster,* this entire question is still under investigation.

In general the emigration response behavior of *D. busckii* measured in the Sakai system is a composite of both dispersal and migration components. In that sense, the overall emigration response is like that of *D. melanogaster.* It is clear, however, that *only* by assessing the emigration responses under the four environmental configurations can the *underlying nature* of the emigration response behavior be ascertained for either species. As will

be discussed below, it is this underlying nature which is crucial for interspecific comparisons.

These two species do not differ significantly in their emigration response behaviors averaged across the four environmental configurations. While interspecific differences can be shown for the emigration response measured in specific configurations (e.g., *D. melanogaster* has a greater response than *D. busckii* for the high tubes in the dark), the crucial difference between these species derives from the comparison of the response spectra of their emigration response behaviors. The *response spectrum* of a behavior is the plasticity of the measured behavioral response with respect to specified environmental perturbations. Behavioral plasticity is the tendency of a behavioral phenotype to change in form or intensity in response to alterations in the environment. Such plasticity reflects the norm of reaction of the genetic system underlying the behavior in question (Dobzhansky, 1970). Rockwell and Seiger (1973) pointed out that the response spectrum of a given behavior is most important in research directed at the elucidation of the underlying mechanisms or evolutionary significance of a given behavior.

The emigration response behavior of *D. busckii* is plastic with respect to tube height but not with respect to lighting condition. The emigration response behavior of *D. melanogaster* is plastic with respect to both tube height and lighting condtion. Considering the four environmental configurations, then, it appears that the emigration response behavior of *D. busckii* is less plastic than that of *D. melanogaster*. It follows that with respect to these environmental perturbations, the norm of reaction of *D. busckii* is narrower than that of *D. melanogaster* for emigration response behavior. Considering the joint effects of the two factors on the response, it also appears that the plasticity (and, hence, norm of reaction) of *D. busckii* is less complex. It will be recalled that in *D. busckii* the effects of tube height were independent of lighting condition. In *D. melanogaster,* the effect of tube height was modulated by lighting condition.

Overall the norm of reaction of *D. busckii* appears to be narrower and less complex than that of *D. melanogaster* for this behavior. There is no doubt that such differences in plasticity and norm of reaction are related to differences in genetic architecture between these two species. The results presented here are consistent with the possibility that the reduced plasticity of this behavior in *D. busckii* derives directly from the reduced heterozygosity of this species. Formal demonstration of that specific relationship awaits further investigation.

Since plasticity is, in general, a product of the genetic architecture underlying a given behavioral trait, the level of plasticity must ultimately derive from the evolutionary history and ecological requirements of a species. Similarly, interspecific differences in plasticity must derive from interspecific differences in these two factors. In fact, a portion of interspecific dif-

ferences in genetic architecture (and plasticity) may reflect the action of selection directed at the level of behavioral plasticity itself (Emlen, 1973; Rockwell and Cooke, 1977). It is tempting to relate the differences in plasticity demonstrated in this work to differences in the evolutionary histories and ecologies of these two species. Such speculation, however, must await further clarification of the evolutionary role of dispersal and migration in this genus. It is clear from this work that studies attempting such clarification must consider the plasticity and, hence, the norm of reaction of emigration response behavior to be at least as important as the overall mean behavior.

Acknowledgments

I wish to thank John Emlen, Joe Griswold, Louis Levine and David Miller for their useful comments on an earlier version of this paper. This work was supported in part by a PSC-BHE award (RF11611) and through the good graces of James Organ, Chairman of Biology, City College.

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Footnote

[1] Contribution 2 from the Theoretical Biology Study Group at City College of New York.

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SCIENTIFIC NOTE

SYNONYMY OF THE GENUS *EUPLUSIA* MOURE UNDER *EUFRIESIA* COCKERELL (HYMENOPTERA, APIDAE, EUGLOSSINI)

The genus *Eufriesia* was originally based on the single species, *pulchra*. Subsequently, another species, *lucifera* Kimsey, was added. It was distinguished from the genus *Euplusia* by the broad flat scutellum, entire head and T-III-VI or VIII brightly metallic with erect yellow setae, and the rest of the body black with black setae.

On comparison of male genitalia of *Eufriesia pulchra* (F. Smith) and *lucifera* Kimsey with the male genitalia of *Euplusia* species, I find no differences to support the separation of these two genera. Unlike other Euglossini, both of these "genera" have strongly bilobed gonostyli and trilobed gonocoxae.

Many external characteristics are also remarkably similar. Examination of the entire genus *Euplusia* reveals a number of species with the same color pattern as *Eufriesia,* including *formosa* (Mocsáry) and *theresiae* (Mocsáry) and other species with a broad flat scutellum, including *violacea* (Blanchard) and *chalybaea* (Friese). The genera share the following external characteristics, which distinguish them from all other euglossines: male hindtibial slit reaching apex; male midtibia with two adjacent felty patches; face brightly metallic without white maculations, and female with a corbicula.

The differences between these two groups are of species value only. *Eufriesia pulchra* and *lucifera* actually appear to belong to a species group containing four species of *Euplusia*.

The genus *Eufriesia* described by Cockerell (1908) has priority over *Euplusia* Moure (1943) which was a replacement for the preoccupied *Plusia* Hoffmannsegg (1817).

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SOME LARVAE OF ORTHOCLADIINAE, CHIRONOMIDAE FROM BROOKS RANGE, ALASKA WITH PROVISIONAL KEY (DIPTERA)

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Reconnaissance samples of benthic invertebrates from two arctic-alpine streams, the Dietrich and Atigun Rivers, Alaska were dominated by Chironomidae larvae (Slack and others, 1976, 1977, 1979). In both rivers the headwaters were dominated by the chironomid subfamily Diamesinae whereas Orthocladiinae predominated further downstream. Although chironomids are known for their abundance in arctic freshwaters (Downes, 1962, 1964; Hobbie, 1973), little taxonomic information is available for Alaskan species. The present report describes and provides a key for the larvae of eleven taxa in the subfamily Orthocladiinae. A similar report on the Diamesinae and a single Podonominae from the same area is in preparation.

The Atigun River flows northward and the Dietrich River flows southward, from the Continental Divide in the Brooks Range. The trans-Alaska pipeline corridor traverses both drainage basins (Fig. 1), but the collections on which this study is based were made in August 1971 before the start of pipeline and road construction.

Methodology

Samples were preserved in 40 percent isopropyl alcohol when collected, and were later separated in the laboratory from detritus by sugar flotation (Anderson, 1959). The introductory keys for chironomid larvae prepared by Mason (1973) and Beck (1968) were most useful because they indicated the morphological characters of greatest value in the separation of species. Other helpful keys were those of Johannsen (1937), Chernovskii (1949), Roback (1957) and Pankratova (1970, in Russian).

The chironomid larvae were first sorted into visually distinct groups. A sample from each group was prepared for microscopic examination by bleaching in hot 10 percent KOH (potassium hydroxide) solution to dissolve soft body tissues. Each specimen was then placed ventral side up on a glass slide in CMC-10[1] mounting medium and pressed under a 12 mm diameter coverslip (Greeson and others, 1977). The illustrations for each taxon are tracings from Polaroid photomicrographs. The heavy backing of the Polaroid paper was carefully peeled from the prints and the insect parts traced using

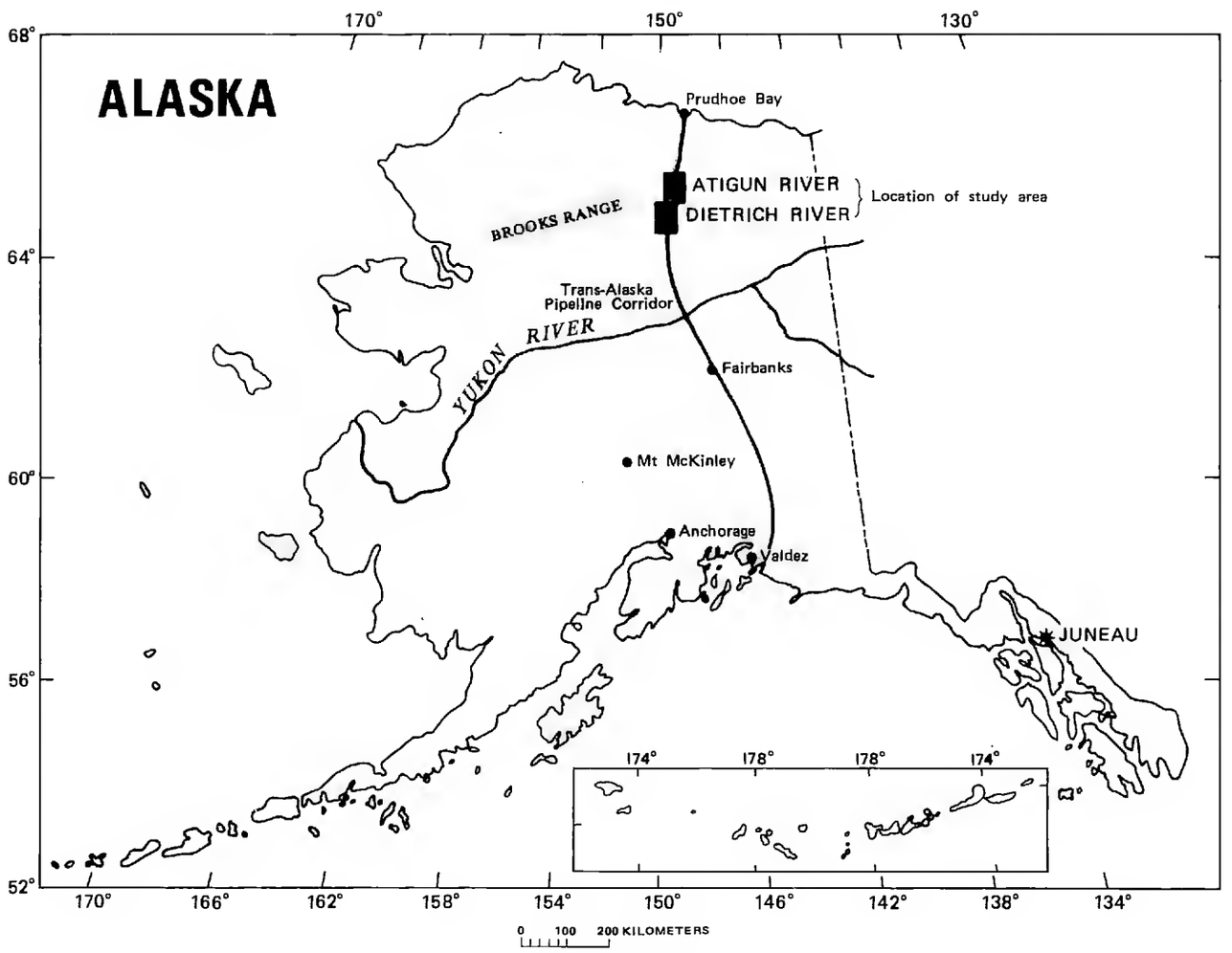

Fig. 1. Location of the Dietrich and Atigun River basins in Alaska.

a light table. Larval measurements were made to the nearest micrometer with a calibrated Whipple disc grid in the ocular of a light compound microscope.

Observations and measurements of the following larval characteristics were used to separate taxa: 1. Antenna: length of each segment, ratio of length of first segment to its width ("ALAW"), length of first segment to that of remaining four segments ("AR"). 2. Labial plate: relative size, shape, and length of midtooth or midteeth; bifurcation of midtooth or number of midteeth; comparison of the width, or length of first pair of lateral teeth to midtooth or midteeth, and total number of pairs of lateral teeth. 3. Mandibles: number of teeth and their relative size distribution. 4. Premandibles: number of digits, their relative size and appearance. 5. Preanal papillae: presence or absence, length versus width. 6. Preanal papillar bristles: length, number, and location.

Instars were estimated using sizes of various morphological features, including body length, head capsule length, and width and length of first antennal segments. To illustrate variability of the averages, standard devia-

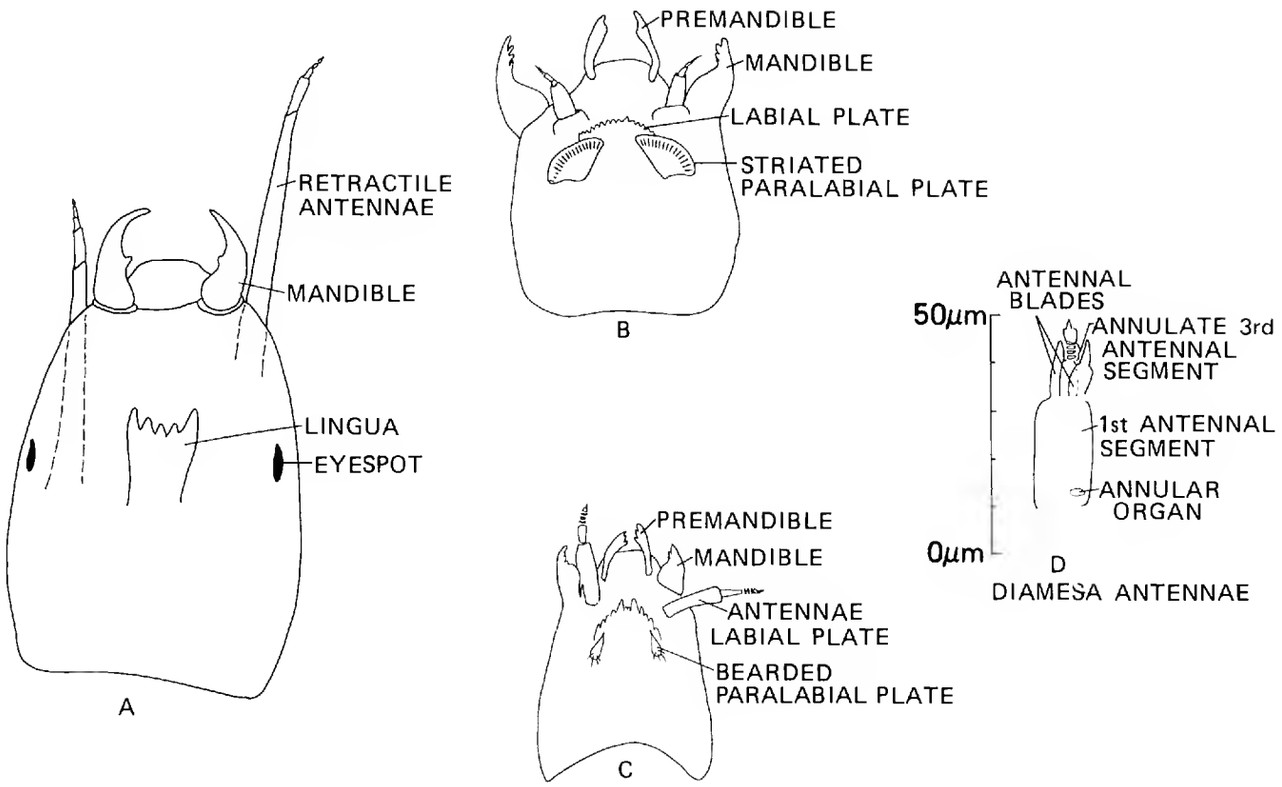

Fig. 2. Head capsule structures (ventral view) used in the identification of larval Chironomidae. (A) Tanypodinae, (B) Chironominae, (C) combined Orthocladiinae and Diamesinae, A, B and C not drawn to scale, (D) antenna of *Diamesa latitarsis* (var. 1) to scale.

tions are reported using the symbol "S.D." Specimens with conspicuously swollen thorax areas were considered to be fourth (last) instars.

It was not possible to assign specific names to many of these larvae, nor is it known whether or not a particular taxon has been described. Species descriptions are based on adults and the immature stages may not be known. The objective of the field study was to enumerate the taxa and their relative abundances in samples of the benthic fauna. Hopefully the information in this paper, which made it possible to distinguish taxa, will be of use to the taxonomist interested in naming adult chironomids and to the ecologist studying benthic invertebrates. Specimens are stored at the U.S. Geological Survey, Western Region Headquarters in Menlo Park, California.

Key to the Common Subfamilies of Chironomidae Larvae and to the Genera of Some Orthocladiinae From Reconnaissance Samples, Dietrich and Atigun Rivers, Brooks Range, Alaska, August 1971

1. Head capsule with fork-shaped lingua; antennae long, often ⅓ length of head or longer, retractile (Fig. 2A) ..... Tanypodinae
   Head capsule without fork-shaped lingua, labial plate present (Fig. 2B and 2C); antennae not retractile 2

2. Premandible absent; preanal papillae at least 3 times longer than wide ..... Podonominae
   Premandibles present (Fig. 2B and 2C) 3
3. Paralabial plates present, usually large, conspicuous and striated (Fig. 2B) ..... Chironominae
   Paralabial plates usually absent, if present paralabial plates without striations, although sometimes bearded (Fig. 2C) 4
4. Third segment of antenna annulate (ringed) (Fig. 2C and 2D); premandibles usually with more than three digits ..... Diamesinae
   Third segment of antenna not annulate; premandibles usually with one or two and sometimes three digits 5
5. Generally freshwater, occasionally terrestrial ..... Orthocladiinae (exclusive of Clunionini) 6
   Generally marine ..... Telmatogetoninae and the Orthocladiinae tribe Clunionini
6. Antennae at least one-half as long as head; body less than 5 mm long; antennae four segmented (Fig. 13A) ..... *Corynoneura* (Winnertz) Edwards Alaska sp. I (Fig. 13)
   Antennae less than one-half as long as head; body longer than 5 mm 7
7. Labial plate with an even number of teeth; midteeth may appear truncate 8
   Labial plate with an odd number of teeth; midtooth rarely truncate 12
8. Premandibles with more than one lobe; usually two or three (Figs. 11D, 12D) ..... *Chaetocladius* (Kieffer) 9
   Premandibles with a single broad, apical lobe (Fig. 3D) ..... *Eukiefferiella* Thienemann 10
9. Midteeth of labial plate longer than first pair of lateral teeth (Fig. 10B) ..... *Chaetocladius* Alaska sp. I (Fig. 10)
   Midteeth of labial plate short, about one-half as long as first pair of lateral teeth (Fig. 11B) ..... *Chaetocladius* Alaska sp. II (Fig. 11)
10. Midteeth of labial plate rounded apically (Fig. 3B); mandibles usually with one or three long serrations on basal inner margin (Fig. 3C) ..... *Eukiefferiella* Alaska sp. I (Fig. 3)
    Larva with characters not as above 11
11. Midteeth of labial plate not truncate; preanal papillae present, about as long as wide; preanal papillary bristles long, about 600 μm long, in fourth instar (Fig. 5B and E) ..... *Eukiefferiella bavarica* Goetghebuer (Fig. 5)
    Midteeth of labial plate usually truncate; preanal papillae absent or

nearly so; preanal papillary bristles short and weak, about 100 μm long in fourth instar (Fig. 4B and E) ..... *Eukiefferiella cynaea* Thienemann (Fig. 4)

12. Paralabial plates present; premandibles with three lobes (Fig. 12B and D) ..... *Parakiefferiella* Thienemann, Alaska sp. I (Fig. 12)

Paralabial plates absent; premandible with less than three lobes .. .. Genus *Orthocladius* Kieffer 13

13. Midtooth of labial plate about two times as wide as first lateral tooth; premandible with cleft near apical end; location of Lauterborn organs uncertain; labial plate with six pairs of lateral teeth ..... *Orthocladius* s. str. (Fig. 9)

Labial plate with more than six pairs of lateral teeth; or antennae with sessile Lauterborn organs at third antennal segment (Fig. 6A) 14

14. Labial plate with six pairs of lateral teeth; sessile Lauterborn organs at third antennal segment (Fig. 6A) .... *Orthocladius* (*Euorthocladius*) Thienemann Alaska sp. I (Fig. 6)

Labial plate with more than six pairs of lateral teeth 15

15. Midtooth of labial plate narrow, about as wide as first lateral tooth; margin of labial plate concave (Fig. 7B); mandibles with all teeth of equal length (Fig. 7C) .... *Orthocladius* (*Euorthocladius*) Thienemann Alaska sp. II (Fig. 7)

Midtooth of labial plate broad, about three times as wide as first lateral tooth, labial plate convex (Fig. 8B); apical tooth of mandible much larger than other mandibular teeth (Fig. 8C) .... *Orthocladius* (*Euorthocladius*) Thienemann Alaska sp. III (Fig. 8)

Orthocladiinae

Eukiefferiella Thienemann

Larva, Goetghebuer 1932, in Pankratova 1970.

Eukiefferiella Alaska sp. I (Fig. 3)

Three instars determined; body length of largest instar (fourth) 2.8–6.0 mm (average 4.1 mm, n = 4, S.D. = 1.41 mm); of intermediate instar (third) 1.9–4.0 mm (average 2.78 mm, n = 49, S.D. = 0.54 mm); and of smallest instar (second) 1.6–3.6 mm (average 1.9 mm, n = 22, S.D. = 0.41 mm). Head capsule of largest instar average 0.33 mm long and 0.21 mm wide (n = 12, S.D. = 0.06 and 0.05 mm). Body color of preserved specimens yellow during first few weeks of storage, after storage with differing amounts of leaf and other detritus, many were brown. Head capsules brown, darker brown with longer storage.

Length of antennal segments of largest instar (fourth) (Fig. 3A), 50: 14:

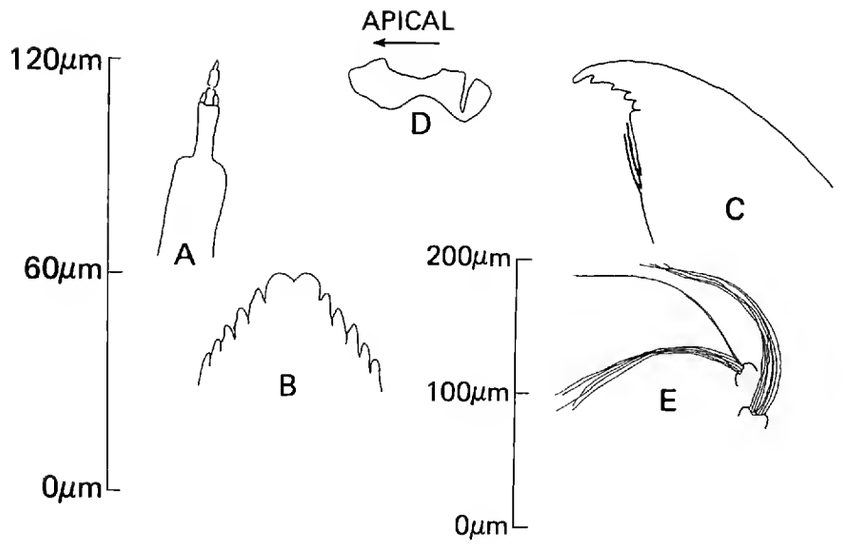

Fig. 3. *Eukiefferiella* Alaska sp. I. (A) antennae, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillae and papillar bristles.

5: 5: 4 μm (n = 4, S.D. = 7.3: 1.7: 0.96: 0.96: 0.82 μm); width of first segment 19 μm (n = 5, S.D. = 2.39 μm); AR = 1.86, S.D. = 0.30, ALAW = 2.64, S.D. = 0.29. Length of antennal segments of intermediate instar (third) 24: 11: 3: 5: 4 μm (n = 60: 57: 57: 57: 57, S.D. = 3.65: 1.23: 1.22: 0.75: 0.71 μm); width of first antennal segment 11 μm (n = 60, S.D. = 1.95 μm); AR = 1.11, S.D. = 0.12, ALAW = 2.29, S.D. = 0.29). Length of antennal segments of smallest instar (second) 13: 9: 2: 3: 3 μm (n = 22, S.D. = 2.40: 1.22: 0.79: 0.74: 0.79 μm); width of first antennal segment 8 μm (n = 22, S.D. = 1.05 μm); AR = 0.76, S.D. = 0.17; ALAW = 1.69, S.D. = 0.37.

Labial plate (Fig. 3B) with midteeth divided, each midtooth rounded apically, much wider than laterals (division not distinct on worn specimens). Five pairs of pointed lateral teeth.

Mandibles (Fig. 3C) with five teeth, progressively smaller from apical tooth to basal tooth. Basal tooth actually a dark area on the apical part of rounded basal section of mandible. Premandible (Fig. 3D) with apical end stout and broad, basal part or attached end convoluted.

Preanal papillae short, when present wider than long. Usually six bristles can be seen at apex of papillae (Fig. 3E); two bristles are shorter than the other four. The four longer bristles on the largest instar (fourth) about 300 μm long (n = 5); intermediate instar (third) 189 μm (n = 65, S.D. = 72.4 μm); and for the smallest instar (second) 136 μm (n = 11, S.D. = 37.6 μm).

Microscope slides were prepared for 149 individual specimens. Detailed measurements were made on 85 specimens. A total of 811 specimens of *Eukiefferiella* Alaska sp. I were estimated from 36 samples collected at 12 sampling sites.

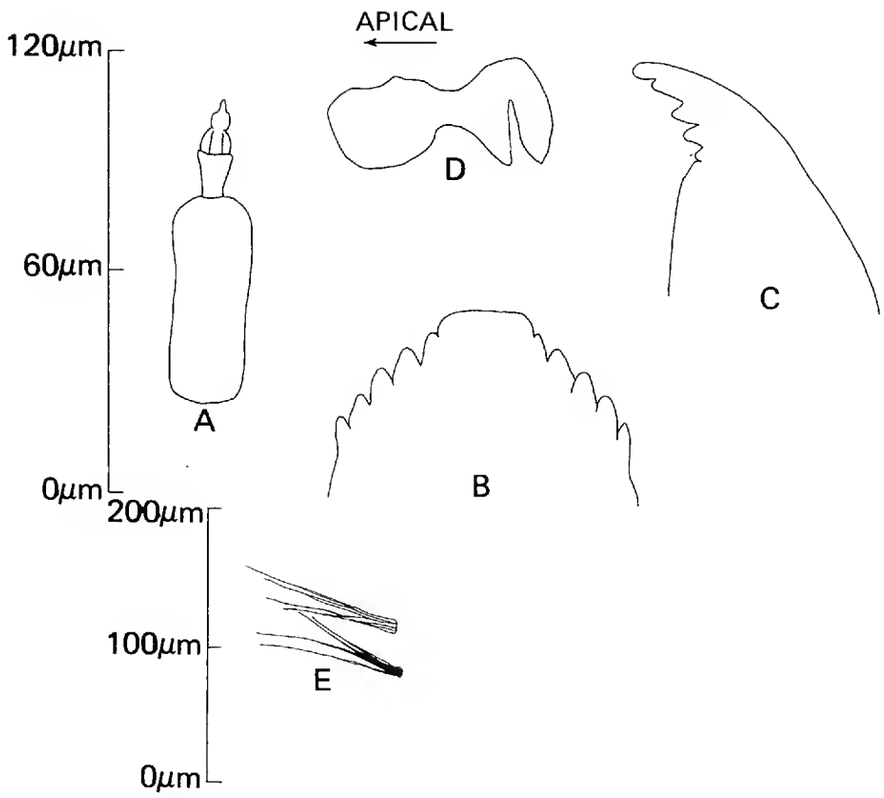

Fig. 4. *Eukiefferiella cynaea,* Thienemann. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillar bristles.

Eukiefferiella cynaea Thienemann
(Fig. 4)

Larva, Thienemann 1936, in Thienemann 1954.

Three instars determined; body length of largest instar (fourth) 3.8–5.7 mm (average 4.73 mm, n = 6, S.D. = 0.66 mm); of intermediate instar (third) 2.0–4.0 mm (average 3.10 mm, n = 45, S.D. = 0.51 mm); and of smallest instar (second) 1.4–2.5 mm (average 1.93 mm, n = 11, S.D. = 0.41 mm). Head capsule of largest instar average 0.35 mm long and 0.25 mm wide (n = 6, S.D. = 0.028 mm and 0.055 mm); of intermediate instar, 0.22 mm long and 0.16 mm wide (n = 41, S.D. = 0.035 and 0.032 mm); and of smallest instar 0.18 mm long and 0.13 mm wide (n = 11, S.D. = 0.041 mm and 0.093 mm). Body color yellow to dark yellow or gray, some with banded appearance (this occurred on many specimens of several taxa where that part of an overlapping abdominal sclerite was darker than the remainder of the sclerite). Usually, specimens were darker dorsally. Head capsules light brown to brown.

Antennae of largest instar (fourth) (Fig. 4A), length of antennal segments 50: 11: 4: 5: 4 μm (n = 7: 6: 6: 6: 6, S.D. = 3.36: 1.63: 1.94: 0.41: 1.10 μm); width of first antennal segment 17 μm (n = 7, S.D. = 1.25 μm); AR = 2.01, S.D. = 0.20; ALAW 2.97, S.D. = 0.21. Length of antennal segments of

intermediate instar (third) 24: 11: 3: 4: 4 μm (n = 45: 42: 42: 42: 42, S.D. = 2.08: 1.03: 1.29: 0.07: 0.63 μm); width of first antennal segment 11 μm (n = 45, S.D. = 0.97 μm); AR = 1.13, S.D. = 0.177; ALAW = 2.23, S.D. = 0.26). Length of antennal segments of smallest instar 16: 10: 3: 4: 3.5 μm (n = 11, S.D. = 2.17: 1.13: 0.87: 1.0: 0.69 μm); width of first antennal segment 9 μm (n = 11, S.D. = 1.54 μm); AR = 0.82, S.D. = 0.136; ALAW = 1.83, S.D. = 0.213.

Labial plate (Fig. 4B) of practically all specimens had midtooth truncate (probably there were two teeth before wear) (Fig. 4B), some specimens with two teeth were otherwise very similar to those with truncate midtooth, so are placed in a single taxon. Truncate area 4 to 5 times width of base of lateral teeth. Five pairs of pointed lateral teeth present with first pair usually showing apical wear.

Mandibles (Fig. 4C) with 5 teeth, progressively smaller from apical tooth to proximal tooth; antennae about same length as mandibles. Premandibles (Fig. 4D) with apical end stout and broad, basal part convoluted.

Preanal papillae absent or nearly so. Four weak bristles present at papillae sites (Fig. 4E); 105 μm long (n = 7, S.D. = 25.3 μm) for largest instar (fourth); 90 μm long (n = 66, S.D. = 21.5 μm) for intermediate instar (third); and 85 μm (n = 11, S.D. = 22.8 μm) for smallest instar (second).

Microscope slides were prepared for 117 individual specimens. Detailed measurements were made on 84 specimens. A total of 581 specimens of *E. cynaea* were estimated from 36 samples at 12 sampling sites.

Eukiefferiella bavarica Goetghebuer
(Fig. 5)

Larva, Thienemann 1935, in Pankratova 1970.

Three instars determined; body length of largest instar (fourth) 3.4–6.0 mm (average 4.69 mm, n = 24, S.D. = 0.68 mm; of intermediate instar (third) 3.0–3.7 mm (average 3.38 mm, n = 12, S.D. = 0.22 mm); and of smallest instar 1.6–2.5 mm (average 2.20, n = 3, S.D. = 0.52 mm). Head capsule of largest instar average 0.36 mm long and 0.25 mm wide (n = 24, S.D. = 0.03 mm and 0.023 mm); of intermediate instar 0.30 mm long and 0.23 mm wide (n = 12, S.D. = 0.04 mm and 0.035 mm); and of smallest instar 0.18 mm long and 0.15 mm wide (n = 3, S.D. = 0.052 mm and 0.05 mm). Body color of preserved specimens light yellow during the first few weeks of storage, after storage with leaf and other detritus, light brown. Head capsules brown to dark brown.

Antennae (Fig. 5A) with first segment long compared to other *Eukiefferiella* taxa from these samples. Length of antennal segments of largest instar (fourth) 66: 14: 4: 6: 5 μm (n = 15, S.D. = 5.73: 1.79: 0.96: 0.86: 0.72 μm); width of first antennal segment 19 μm (n = 15, S.D. = 2.24 μm); AR =

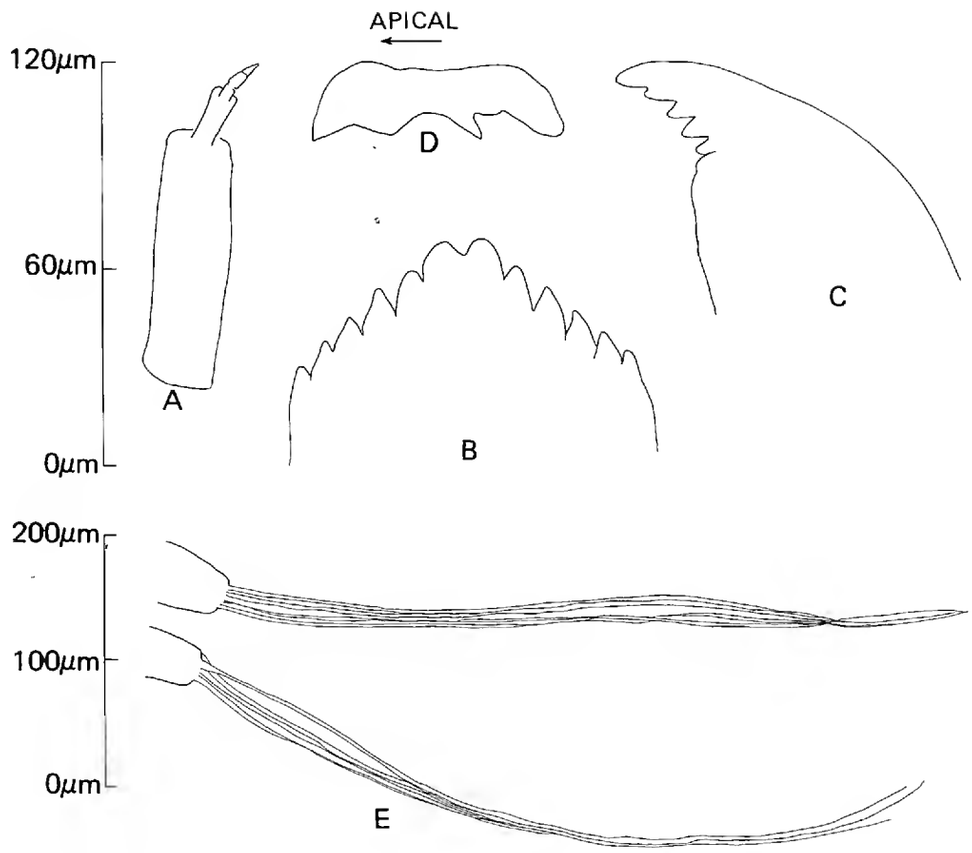

Fig. 5. *Eukiefferiella bavarica* Goetghebuer. (A) antenna, (B) labial plate, (C) left mandible, (D) left premandible, (E) preanal papillae and papillar bristles.

2.28, S.D. = 0.22; ALAW = 3.52, S.D. = 0.42. Length of antennal segments of intermediate instar (third) 44: 16: 4: 6: 4 μm (n = 12, S.D. = 6.06: 1.24: 1.16: 0.57: 0.72 μm); width of first antennal segment 16 μm (n = 12, S.D. = 0.75 μm); AR = 2.89, S.D. = 0.38; ALAW = 2.64, S.D. = 0.75. Length of antennal segments of smallest instar (third) 21: 12: 4: 4: 3 μm (n = 3, S.D. = 5.13: 1.53: 1.15: 1.0: 0.58 μm); width of first antennal segment 11 μm (n = 3, S.D. = 1.53 μm); AR = 0.88, S.D. = 0.26; ALAW = 1.92, S.D. = 0.22).

Labial plate (Fig. 5B) with two large midteeth, 2 to 3 times larger than lateral teeth. Five pairs of lateral teeth.

Mandibles (Fig. 5C) with five teeth progressively smaller from apical tooth to proximal tooth. Premandibles (Fig. 5D) apically stout and broad, convoluted at the base where attached.

Preanal papillae present (Fig. 5E) about as wide as long approximately 35 μm long and 37 μm wide. Six bristles attached to end of papillae (in largest instar, fourth) 600 μm long (n = 10, S.D. = 125.0 μm), one bristle attached to side of papillae 150 μm long (n = 8, S.D. = 37.8 μm). Apical bristles for intermediate instar (third) 330 μm long (n = 8, S.D. = 61.1 μm); and for smallest instar (second) apical bristles 230 μm long (n = 1).

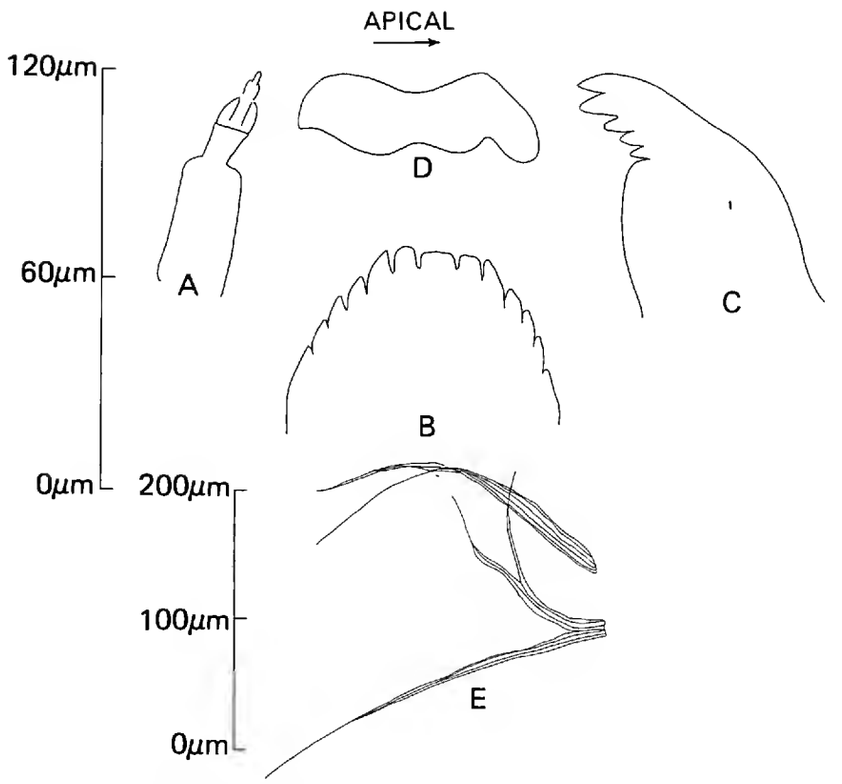

Fig. 6. *Orthocladius* (*Euorthocladius*) Alaska sp. I. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillar bristles.

Microscope slides were prepared for 50 individual specimens. Detailed measurements were made on 39 specimens. A total of 139 specimens of *E. bavarica* were estimated from 36 samples collected at 12 sampling sites.

Genus *Orthocladius* Kieffer
Subgenus *Euorthocladius* **Thienemann**

Larva, as per O. A. Saether, written communication, 1973

Orthocladius (*Euorthocladius*) Alaska sp. I
(Fig. 6)

Three instars determined; body length of largest instar (fourth) 3.5–5.5 mm (average 4.5 mm, n = 4, S.D. = 0.90 mm); of intermediate instar (third) 2.3–3.0 mm (average 2.65 mm, n = 4, S.D. = 0.31 mm); and of smallest instar 1.5–2.8 mm (average 2.30 mm, n = 27, S.D. = 0.44 mm). Head capsule of largest instar average 0.26 mm long and 0.14 mm wide (n = 2); of intermediate instar, 0.24 mm long and 0.19 mm wide (n = 4, S.D. = 0.042 mm and 0.013 mm); of smallest instar (second) 0.21 mm long and 0.16 mm wide (n = 26, S.D. = 0.043 mm and 0.026 mm). Body color of preserved specimens light green or light yellow, later brown after storage with leaf and other detritus. Head capsules light brown.

Length of antennal segments of largest instar (fourth) (Fig. 6A), 34: 9: 6:

3: 4 μm (n = 4: 3: 3: 3: 3, S.D. = 4.35: 1.15: 2.0: 0.58: 0.58 μm); width of first antennal segment 18 μm (n = 4, S.D. = 4.24 μm). Length of antennal segments of intermediate instar (third) 23: 11: 3: 4: 4 μm (n = 4, S.D. = 1.71: 1.89: 0.96: 0.96: 0.58 μm); width of first antennal segment 12 μm (n = 4, S.D. = 1.41 μm). Length of antennal segments of smallest instar (second) 17: 9: 3: 3: 3 μm (n = 24: 24: 23: 23: 23, S.D. = 2.95: 0.66: 1.58: 0.54: 0.39 μm); width of first antennal segment 12 μm (n = 23, S.D. = 1.57 μm); AR = 0.93, S.D. = 0.175; ALAW = 1.41, S.D. = 0.18. Usually sessile Lauterborn organs are present, attached to apical end of second antennal segment and are as long as third antennal segment (Fig. 6A).

Labial plate (Fig. 6B) with midtooth ranging from about one and one-half to twice as wide as the first pair of lateral teeth. The midtooth and first laterals show wear before remainder of laterals, usually are set apart slightly and all three truncate. There are six pairs of lateral teeth.

Mandibles (Fig. 6C) with five teeth, progressively smaller from apical teeth to proximal teeth. Second tooth wider than first tooth, sometimes mandible teeth appear as two large teeth and three small teeth. Premandibles (Fig. 6D) apically with a single tapered lobe.

Preanal papillae absent, or nearly so. Six bristles present at papillae sites (Fig. 6E); 400 μm long (n = 2) on largest instar (fourth); 360 μm long (n = 4, S.D. = 80.1 μm) on intermediate instar (third) and rounded to 315 μm long (n = 24, S.D. = 67.4 μm) on smallest instar (second).

Microscope slides were prepared for 71 individual specimens. Detailed measurements were made on 34 specimens. A total of 785 *O.* (*Euorthocladius*) Alaska sp. I were estimated from 36 samples collected at 12 sampling sites.

Orthocladius (*Euorthocladius*) Alaska sp. II
(Fig. 7)

Two instars determined; body length of largest instar (fourth) 3.0–6.4 mm (average 4.15 mm, n = 11, S.D. = 1.19 mm); of smaller instar 3.5 mm long (n = 1). Head capsule of largest instar 0.33 mm long and 0.29 mm wide (n = 2). Body color of preserved specimens dark yellow-brown or brown, some with banded appearance.

Antennae (Fig. 7A) with first segment short and wide compared with other specimens from these samples. Length of antennal segments of largest instar (fourth) 28: 11: 3: 3: 3 μm (n = 12: 12: 11: 11: 11, S.D. = 2.61: 1.44: 1.19: 0.54: 0.65 μm); width of first antennal segment 21 μm (n = 11, S.D. = 2.91 μm); AR = 1.39, S.D. = 0.24; ALAW = 1.37, S.D. = 0.14.

Labial plate (Fig. 7B) with midtooth only slightly wider than lateral teeth. Margin of labial plate on these specimens concave. Nine pairs of lateral teeth present.

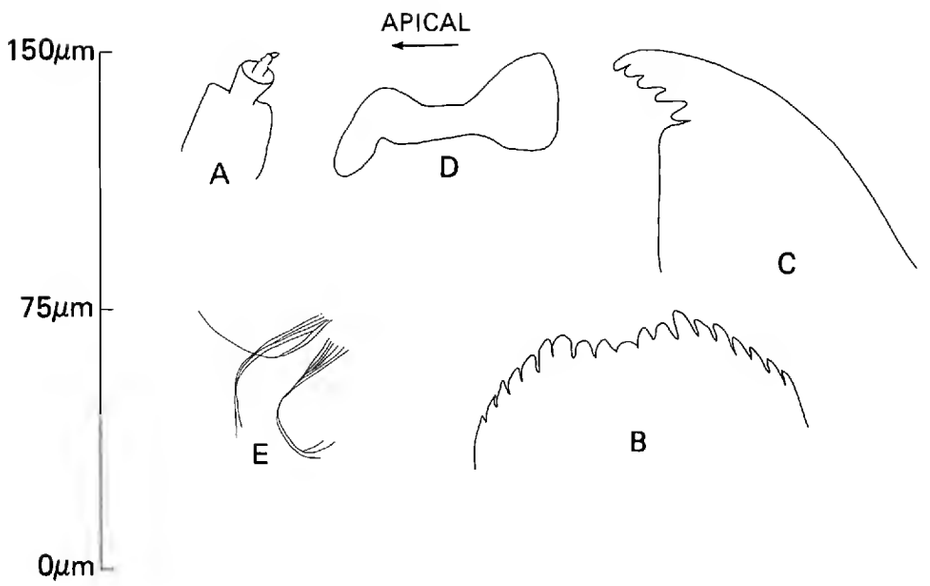

Fig. 7. *Orthocladius* (*Euorthocladius*) Alaska sp. II. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillar bristles.

Mandibles (Fig. 7C), most showing wear, with teeth progressively smaller (about same size on worn specimens) from apical teeth to proximal teeth. Premandibles (Fig. 7D) slightly divided apically.

Preanal papillae absent; 4 pairs of weak bristles at papillae sites (Fig. 7E) average 90 μm (n = 7, S.D. = 17.3 μm) on largest instar (fourth); 50 μm (n = 1) on smaller instar (third).

Microscope slides were prepared for 26 individual specimens. Detailed measurements were made on 13 specimens. A total of 58 *O. Euorthocladius* Alaska sp. II were estimated for 36 samples at 12 sampling sites.

Orthocladius (*Euorthocladius*) Alaska sp. III (Fig. 8)

Only seven individuals were estimated from 36 samples collected at 12 sampling sites. Microscope slides were prepared and detailed measurements made on two specimens.

Both measured specimens were believed to be the same instar. Body lengths 3.5 and 4.6 mm. Head capsule of larger specimen 0.45 mm long and 0.32 mm wide. Body color of preserved specimens orange-brown and head capsule brown.

Antennae (Fig. 8A) for larger specimen with first segment was very wide and stout compared to specimens from other taxa in these samples. Length of antennal segments for the larger specimen 49: 7: 3: 2: 4 μm, width of first antennal segment 37 μm; AR = 3.06; ALAW = 1.32. Width of first antennal segment about three to four times wider than width of second segment.

Labial plate (Fig. 8B) with midtooth three to four times wider than lateral

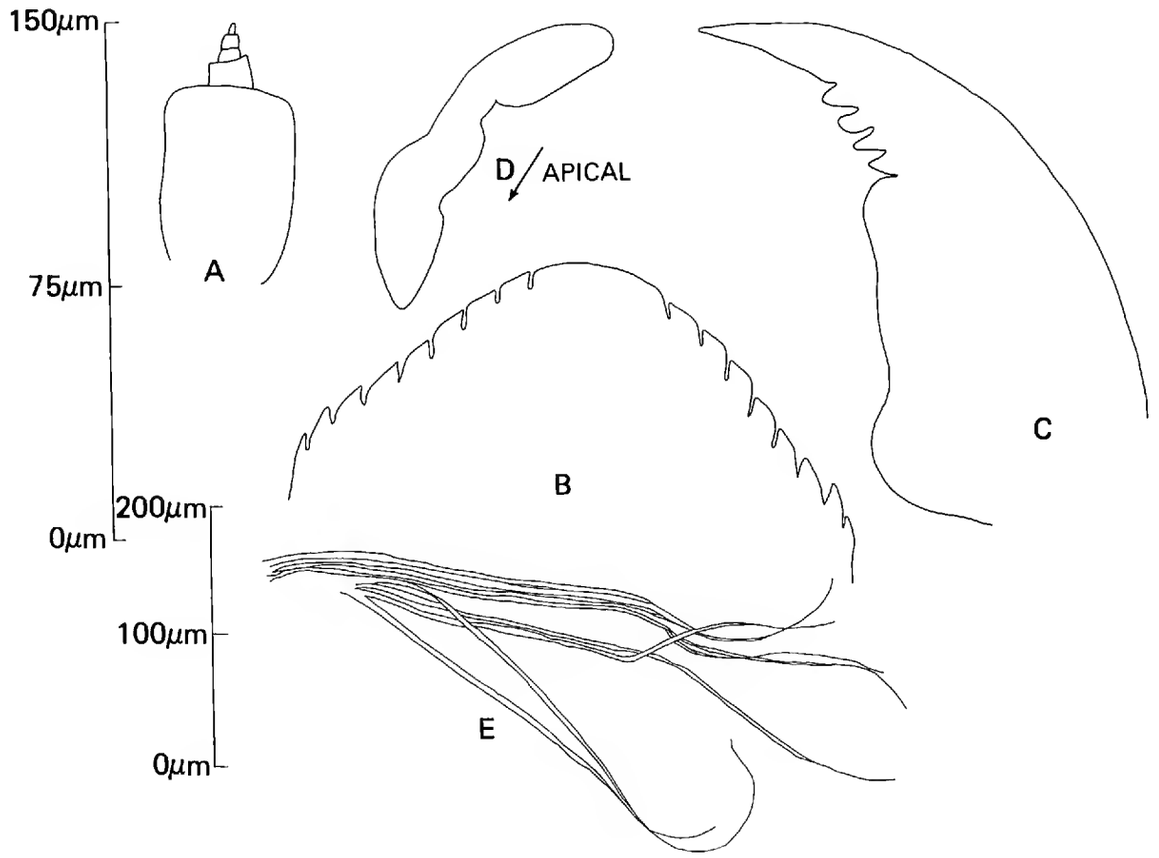

Fig. 8. *Orthocladius* (*Euorthocladius*) Alaska sp. III. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillar bristles.

teeth. Nine pairs of lateral teeth. Margin of labial plate smooth, slightly worn with tips of lateral teeth pointed toward the midtooth.

Mandibles (Fig. 8C) with a very large, scythe-shaped apical tooth and four, much smaller, proximal teeth. Premandibles (Fig. D) a large tapered lobe apically.

Preanal papillae absent; 4 or 5 bristles (Fig. 8E) arising from each papillae site about 500 μm long.

Subgenus *Orthocladius* s.str.
(Fig. 9)

Information provided by Ole A. Saether, 1973

Two instars determined; body length of largest instar (fourth) 2.6–6.0 mm (average 4.67 mm, n = 31, S.D. = 0.77 mm); for smaller instar (third) 1.9–3.0 mm (average 2.46 mm, n = 9, S.D. = 0.37 mm). Head capsule of largest instar 0.41 mm long and 0.31 mm wide (n = 30, S.D. = 0.067 mm and 0.048 mm); and of smaller instar 0.24 mm long and 0.18 mm wide (n = 8, S.D. = 0.025 mm and 0.016 mm). Body color of preserved specimens yellow, yellow-brown, some with green tinge to other colors. Head capsules yellow, light brown or yellow-brown.

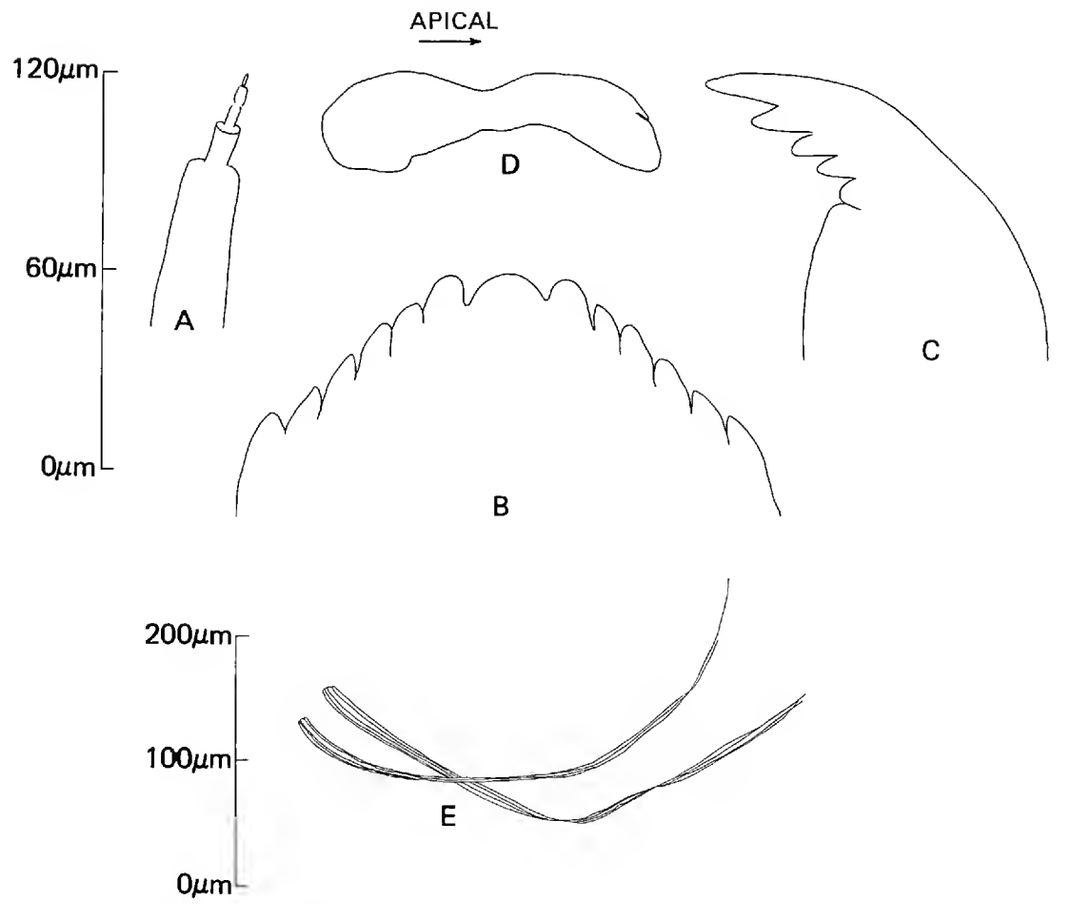

Fig. 9. *Orthocladius* s.str. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillar bristles.

Antennae of largest instar (Fig. 9A) with segment lengths of 49: 14: 6: 5: 4 μm (n = 29: 28: 28: 28: 28, S.D. = 4.18: 2.25: 1.33: 0.99: 0.90 μm); width of first antennal segment 22 μm (n = 27, S.D. = 3.95 μm); AR = 1.77, S.D. = 0.258; ALAW = 2.30, S.D. = 0.387. Length of antennal segments of smaller instar 20: 9: 4: 3: 3 μm (n = 9, S.D. = 4.5: 1.50: 0.53: 0.33: 0.73 μm); width of first antennal segment 12 μm (n = 9, S.D. = 0.93 μm); AR = 1.07, S.D. = 0.103; ALAW = 1.73, S.D. = 0.438.

Labial plate (Fig. 9B) with a wide, rounded midtooth, two to two and one-half times as wide as lateral teeth. There are 6 pairs of lateral teeth, usually the first pair is slightly worn or rounded.

Mandibles (Fig. 9C) with 5 teeth progressively smaller from apical teeth to proximal teeth. Crenulations on the outer margin of the mandibles are prominent on some specimens, weak or absent on others. Premandibles (Fig. 9D), a tapered lobe with a small notch near apex.

Preanal papillae slight (Fig. 9E), always wider than long. Six bristles present at apex of each papilla; 485 μm long (n = 29, S.D. = 123.1 μm) on the largest instar (fourth); 320 μm long (n = 9, S.D. = 14.9 μm) on the smaller instar (third).

Microscope slides were prepared for 41 individual specimens. Detailed

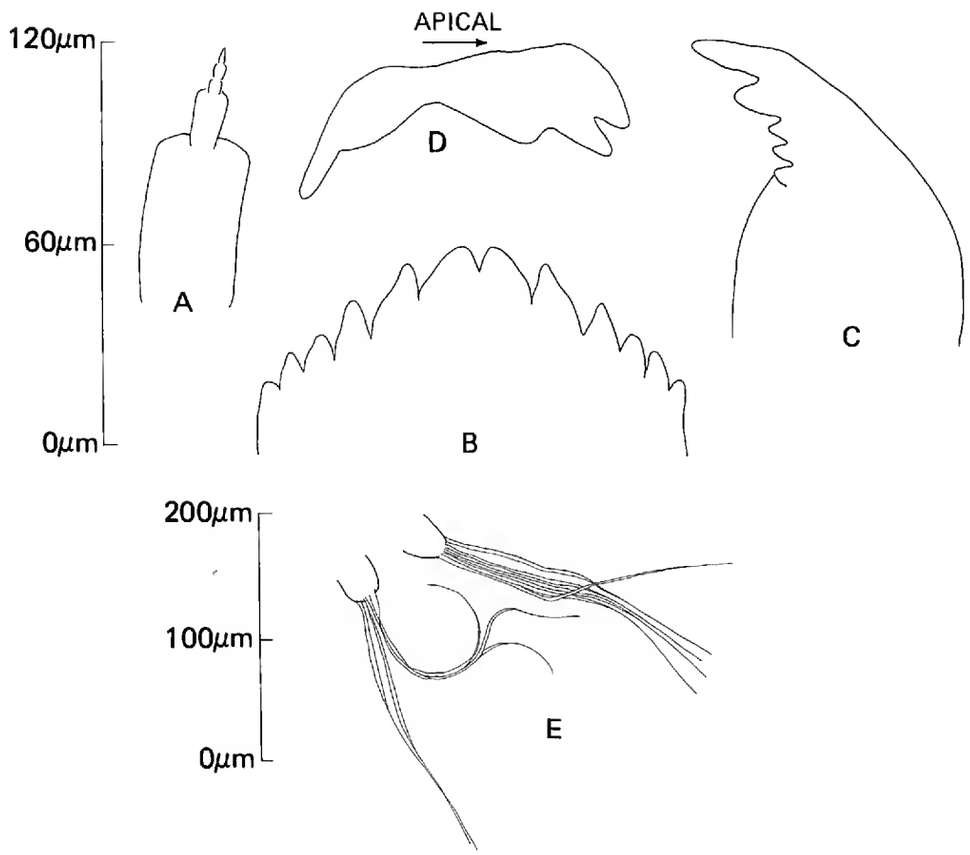

Fig. 10. *Chaetocladius* Alaska sp. I. (A) antenna, (B) labial plate, (C) left mandible, (D) right premandible, (E) preanal papillae and papillar bristles.

measurements were made on 39 specimens. A total of 103 specimens of *Orthocladius* s.str. were estimated from 36 samples collected at 12 sampling sites.

Genus *Chaetocladius* (Kieffer)

Larva, Thienemann 1921, in Pankratova 1970

Chaetocladius Alaska sp. I
(Fig. 10)

One instar determined (third or fourth) body length 3.0–5.4 mm (average 3.97 mm, n = 11, S.D. = 0.70 mm). Head capsule, 0.28 mm long and 0.20 mm wide (n = 11, S.D. = 0.057 mm and 0.041 mm). Body color of preserved specimens yellow-brown, and head capsule brown.

Antennae (Fig. 10A), each segment 36: 10: 5: 4: 3 μm long (n = 13: 13: 11: 11: 11, S.D. = 5.72: 1.55: 1.49: 1.21: 0.92 μm); width of first antennal segment 16 μm (n = 13, S.D. = 2.91 μm); AR = 1.56, S.D. = 0.32; ALAW = 2.23, S.D. = 0.45.

Labial plate (Fig. 10B) with 2 large, dark midteeth and 5 pairs of lateral teeth. Last pair of teeth nearly trilobed single tooth.

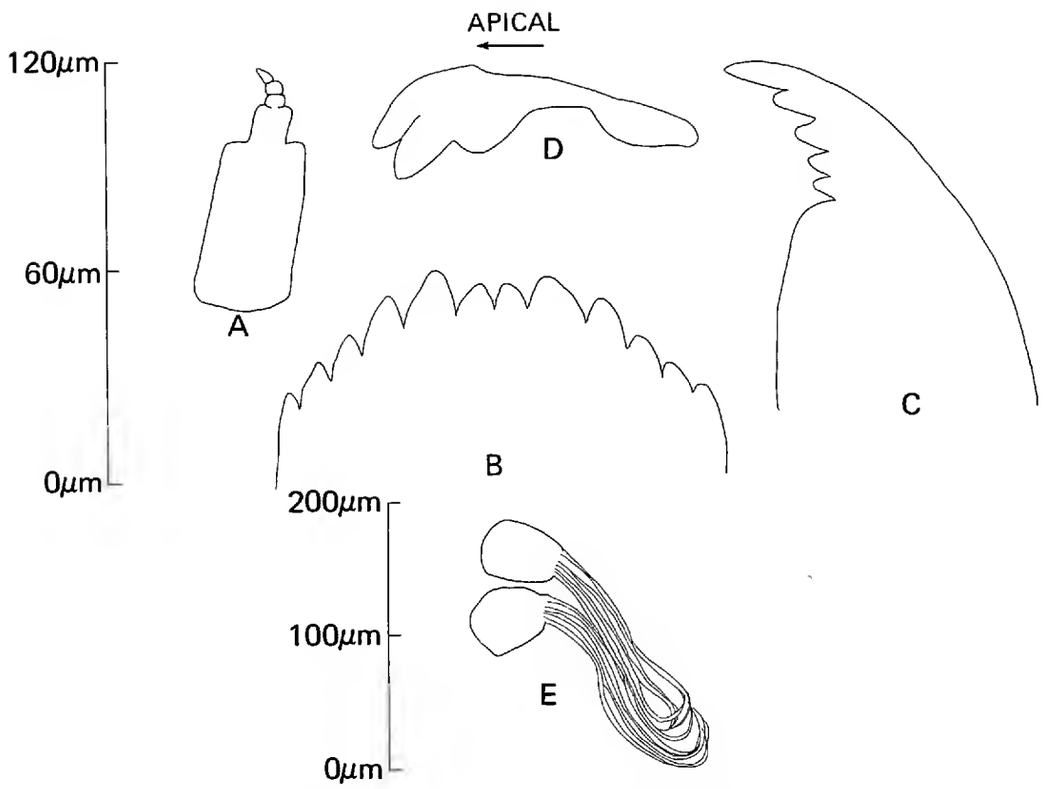

Fig. 11. *Chaetocladius* Alaska sp. II. (A) antenna, (B) labial plate, (C) left mandible, (D) left premandible, (E) preanal papillae and papillar bristles.

Mandibles (Fig. 10C) with 5 teeth, apical tooth large, second tooth one-half size of apical tooth and last three teeth much smaller. Premandible (Fig. 10D) with three lobe-like digits.

Preanal papillae (Fig. 10E) present, about as long as wide (20 μm long and 20 μm wide). Five bristles at apices of papillae, 325 μm long (n = 9, S.D. = 56.6).

Microscope slides were prepared for 15 individual specimens. Detailed measurements were made on 13 specimens. A total of 17 specimens of *Chaetocladius* Alaska sp. I were estimated from 36 samples collected at 12 sampling sites.

Chaetocladius Alaska sp. II
(Fig. 11)

Only a single specimen was taken from 36 samples collected at 12 sampling sites.

Body length of specimen 3.6 mm, head capsule not measured. Body color of preserved specimen banded, brown bands and brown-white between bands, head capsule dark brown.

Antennae (Fig. 11A) length of segments 45: 13: 3: 3: 3 μm; width of first antennal segment 25 μm; AR = 2.05, ALAW = 1.8.

Labial plate as in Fig. 11B. Two midteeth each only one-half as long as

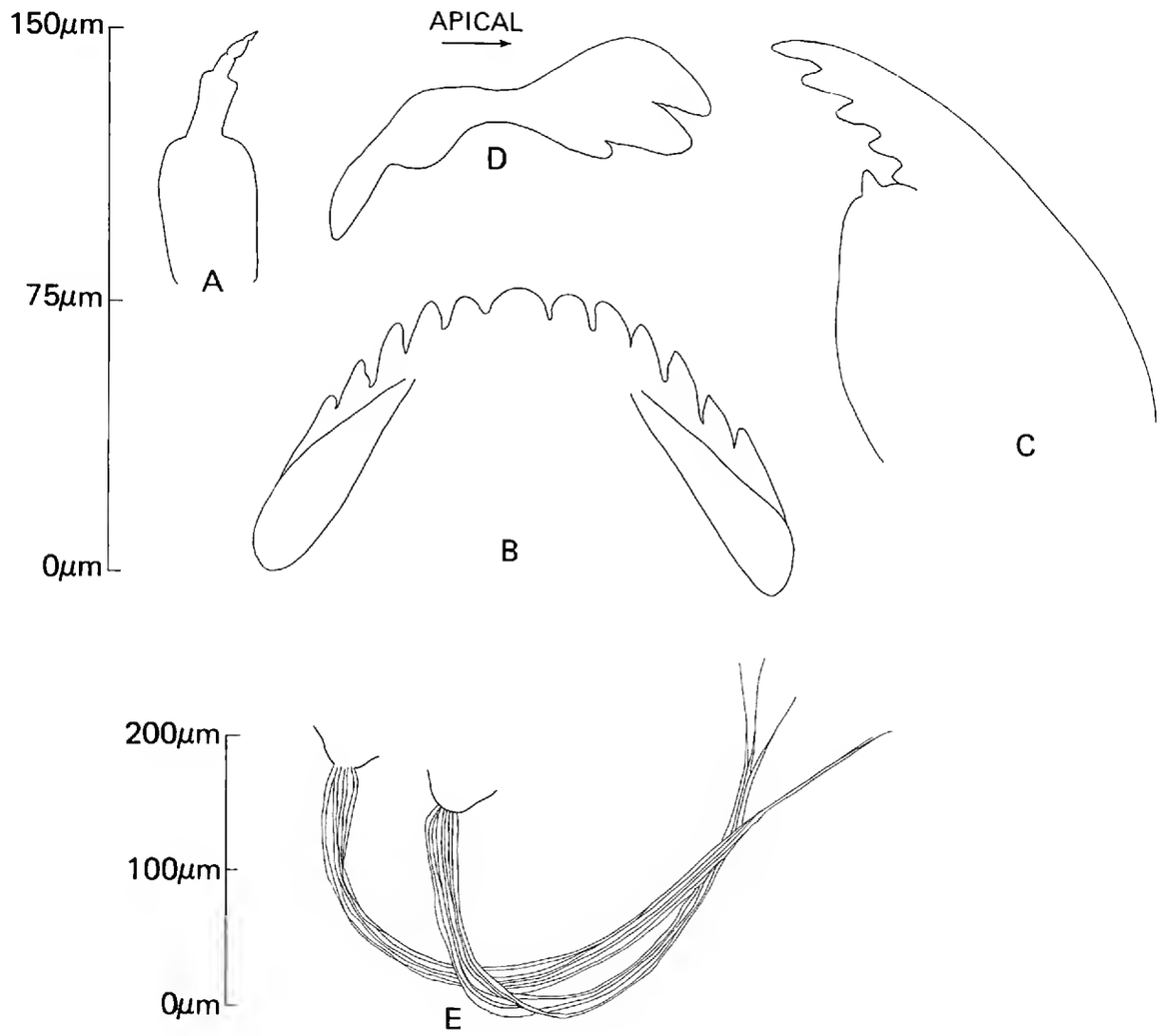

Fig. 12. *Parakiefferiella* Alaska sp. I. (A) antenna, (B) labial plate with paralabials, (C) left mandible, (D) right premandible, (E) preanal papillae and papillar bristles.

first or second pairs of lateral teeth. Five pairs of lateral teeth, last three pairs smaller than first two pairs.

Mandibles (Fig. 11C) with five teeth, apical tooth large and remaining four teeth small and progressively smaller from second tooth to proximal teeth. Premandibles (Fig. 11D) with two large tapered lobe-like digits with a lateral (mesad) bulge.

Preanal papillae (Fig. 11E) present, about as long as wide (32 μm long and 35 μm wide) with a robust appearance. Six pairs of bristles about 300 μm long.

Genus *Parakiefferiella* (Thienemann)

Larva, Thienemann 1936, as in Pankratova 1970

Parakiefferiella Alaska sp. I
(Fig. 12)

Only 11 individuals were estimated from 36 samples collected at 12 sam-

pling sites. Microscope slides were prepared for five specimens and detailed measurements made on two specimens.

Body length of five specimens 3.5–4.5 mm (average 4.0 mm, n = 5, S.D. = 0.5 mm). Head capsule 0.38 mm long and 0.28 mm wide (n = 2). Body color of preserved specimens yellow, head capsule yellow-brown.

Antennae as in Fig. 12A. Length of antennal segments 50: 16: 5.5: 3: 2.5 μm (n = 2); width of first antennal segment 29 μm (n = 2); AR = 1.85; ALAW = 1.72.

Labial plate (Fig. 12B) with a single midtooth one and one-half to two times wider than lateral teeth. Six pairs of lateral teeth present with paralabial plates beginning apically at outer base of second pair of lateral teeth to posterior of the base of the last pair of lateral teeth (paralabial plates not easily detected on these specimens).

Mandibles (Fig. 12C) with five teeth, progressively smaller from apical tooth to proximal tooth. Premandibles (Fig. 12D) with two tapered lobes.

Preanal papillae (Fig. 12E) wider than long (about 20 μm long and 32 μm wide). Four terminal bristles about 425 μm long.

Genus *Corynoneura* (Winnertz) Edwards, in Pankratova 1970

Larva, Pankratova 1970

Corynoneura Alaska sp. I
(Fig. 13)

Only 6 specimens of *C.* Alaska sp. I were estimated from 36 samples collected at 12 sampling sites, all specimens came from one site. One instar determined (third or fourth), body length 1.2 mm long (n = 2). Head capsule of a single specimen 0.14 mm long and 0.11 mm wide. Body color of preserved specimens yellow, head capsule light brown.

Antennae (Fig. 13A) with two annular organs, the first at midpart of first antennal segment and the second about three-fourths the length of first antennal segment from the base. There is a small spur-like blade about 4 μm long at apex of second antennal segment. Antennae with four segments, length of antennal segments 63: 47: 45: 2 μm (n = 2); width of first segment 17 μm; AR = 0.66; ALAW = 3.71.

Labial plate (Fig. 13B) with midtooth small, first pair of lateral teeth much larger than midtooth. Total of 6 pairs of lateral teeth, second pair smaller than third pair, and third pair almost as large as first pair.

Mandibles (Fig. 13C) with five teeth, first tooth smaller than second tooth. Third through fifth tooth progressively smaller. Premandibles (not illustrated) poor on both specimens, possibly divided into two lobes.

Preanal papillae short (Fig. 13E), 4 bristles at apex about 160 μm long. Spines, one group each at dorsal base of each proleg. Each spine group

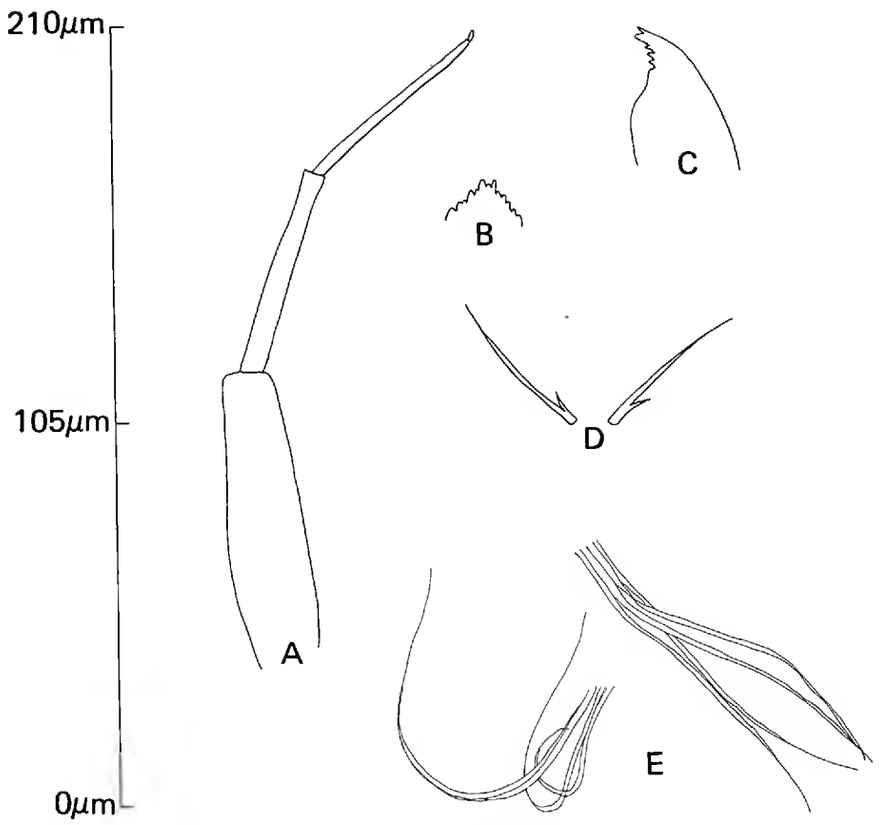

Fig. 13. *Corynoneura* unnamed Alaska sp. I. (A) antenna, (B) labial plate, (C) left mandible, (D) spines, of posterior prolegs, (E) preanal papillar bristles.

(Fig. 13D) with one long spine 48 μm long and a second spine (at base of first spine) 11 μm long.

Acknowledgment

Dr. Ole A. Saether of The Freshwater Institute in Winnipeg, Canada, identified representative samples of each taxon. Most of the drawings were prepared from specimens examined by him.[2]

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Footnote

[1] Mention of trade names or commercial products does not constitute endorsement by the U.S. Geological Survey nor recommendation for use.

[2] Dr. Saether is now Professor of Systematic Zoology at the University of Bergen, Norway.

PAN-PACIFIC ENTOMOLOGIST
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A NEW SPECIES OF *TANARTHRUS* FROM CALIFORNIA (COLEOPTERA: ANTHICIDAE)

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Recently a large series of an undescribed species of *Tanarthrus* was collected along the Leslie salt pans in San Francisco Bay. The distribution of the new species is of interest since the species most similar to it, *T. iselini* Chandler, is found only in central New Mexico. Following the distributional mechanisms proposed in my revision (Chandler, 1975), this distribution suggests a pre-Pleistocene separation of populations.

The species description follows that of Chandler (1975). All measurements are in millimeters. I would like to thank Christine A. Janus-Chandler for checking the manuscript.

Tanarthrus occidentalis, new species
(Figs. 1–2)

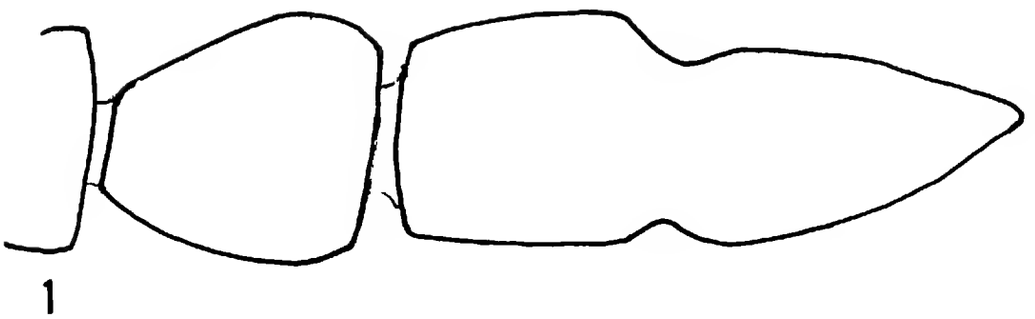
General description.—Elytra usually piceous, fuscous areas may be present to cover basal third and apical fourth; head and pronotum fulvous; elytra feebly ridged and punctate, pubescence directed posteriorly, microreticulation present; pronotal angles rounded, roughly sculptured by punctation, microreticulate between punctures; head subtruncate, base with medial depression, shallow punctures distinct, moderately dense, microreticulation distinct, eleventh antennal segment distinctly constricted, portion before constriction as long as to slightly shorter than tenth, portion after constriction as long as to slightly longer than tenth; length 2.61–3.55.

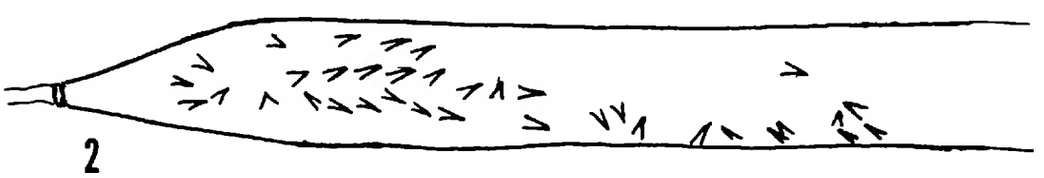
Male holotype.—3.2 km (2 mi) W Newark, California. Head 0.83 long, width behind eyes 0.79, length from base to eyes 0.35, width at antennal bases 0.43, length from base to antennal bases 0.59; basal portion of eleventh antennal segment 0.07 long, after constriction 0.10 long, tenth segment 0.10 long. Pronotum 0.76 long, width at base 0.49, widest point 0.68 at 0.50 from base; collar 0.04 thick, 0.30 wide. Elytra 1.94 long, width at humeri 0.90, scattered erect setae at 40–60 degree angle. Profemur 0.66 long, 0.19 wide, protibia 0.67 long; mesofemur 0.65 long, 0.20 wide, mesotibia 0.65 long; metafemur 0.79 long, 0.21 wide, metatibia 0.72 long.

Genitalia with tegmen as long as phallobase; internal sac with numerous spines; primary gonopore with sclerotized ring.

Female without erect elytral setae.

Relationship.—most similar to *T. iselini* in the medial basal depression of





Figs. 1–2. Fig. 1. Tenth and eleventh antennal segments. Fig. 2. Ventral view of male genitalia.

the head and the erect elytral setae of the male. Separated from *iselini* by the entire antenna being more slender in appearance and both portions of the eleventh antennal segment being longer than wide. In *iselini* the divisions of the eleventh segment appear almost moniliform and the tenth segment and basal portion of the antennal constriction are as long as wide.

Distribution.—Known only from the Leslie salt pans near Newark along San Francisco Bay. HOLOTYPE male, 3.2 km (2 mi) W Newark, off Dumbarton Bridge, Alameda County, California, V-27-1976, C. Y. Kitayama. 33 PARATYPES: 15 males, 5 females, eutopotypical; 1 male, 12 females, same locality, V-15-1978, D. S. Chandler, under debris along salt pans.

The holotype will be deposited in the California Academy of Sciences, with paratypes to be placed in the United States National Museum and the Floyd G. Werner collection, Tucson, Arizona.

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A NEW *EREMOCORIS* FROM CALIFORNIA WITH A KEY TO NORTH AMERICAN GENERA OF DRYMINI (HEMIPTERA-HETEROPTERA: LYGAEIDAE)

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Peculiar species often present problems of placement, and such is the case with a short-winged drymine (Rhyparochrominae) described herein. Specimens of the species, which were collected in northern California on Sargent's Cypress, have been in my collection for several years, and additional specimens were found in the collection of the California Academy of Sciences. The species looks like an *Eremocoris,* but is an unusual member of that genus. It has shorter wings than any other species and is quite uniformly dark reddish brown, lacking the patterns on the pronotum and hemelytra common in the genus. The degree of brachyptery is similar to that of *Togodolentus wrighti* (Van Duzee), and in both species the anterior lobe of the pronotum is much longer than the hind lobe and somewhat swollen. These pronotal characters are associated with the wing modification. There were no macropterous specimens available of either species.

Study was begun to determine if the new cypress bug is an odd *Eremocoris,* or a second species of the monotypic genus *Togodolentus,* or whether *Togodolentus wrighti* itself is merely another peculiar species of *Eremocoris.*

The hind tibia of the cypress bug has along its entire length numerous long, erect hairs that are about three times as long as the measurement across the tibia (see Fig. 1). Sweet (1977) described this condition for *E. ferus* (Say) from eastern North America and used it to distinguish *E. ferus* from *E. borealis* (Dallas). Other *Eremocoris* with long tibial hairs are *E. setosus* Blatchley (eastern U.S., Canada), *E. plebejus* Fallén (Europe, Siberia), and *E. semicinctus* Van Duzee (California, Idaho). These long tibial hairs may have confused E. P. Van Duzee (1921) when he described *E. semicinctus,* for the allotype of his species is a female of the cypress bug described below. *Eremocoris* species with short, appressed tibial hairs, in addition to *E. borealis* cited by Sweet (1977), are *E. depressus* Barber (southeastern U.S.), *E. dimidiatus* Van Duzee (Colorado), *E. obscurus* Van Duzee (western U.S., Canada), and *E. opacus* Van Duzee and *E. inquilinis* Van Duzee (both California). All other North American drymines, and *Togodolentus wrighti,* have short, appressed hairs on the hind tibia.

The long tibial hairs found only in some species of *Eremocoris* may be a synapomorphous character delimiting a holophyletic group within the ge-

nus. If so, placing the cypress bug in *Togodolentus* would make *Togodolentus* polyphyletic, which is contrary to good systematic practice.

Whether *Togodolentus wrighti* is enough like *Eremocoris* species to be placed in the genus is another question. The buccula of most North American drymines appears from the side as a prominent lobe obscuring the base of the labium. Viewed ventrally, the bucculae extend posteriorly as carinae that join to enclose a gular region. In all *Eremocoris,* including the cypress bug, these carinae extend to or nearly to the base of the head, enclosing a posteriorly tapering gular region. In *Togodolentus,* the carinae extend only to the level of the anterior margin of the eye, and the enclosed gular region is parallel-sided.

Further, most North American drymines have the lateral margins of the pronotum to some degree explanate. (*Thylochromus* is an exception.) In *Togodolentus,* the explanate margin is wider than in any other North American drymine (at the middle, wider than the middle part of the second antennal segment). In species of *Eremocoris,* these margins are not as wide as the second antennal segment at its midpoint. Given this information, I conclude that the cypress bug is a true *Eremocoris,* and that the genus *Togodolentus* should be retained.

Eremocoris cupressicola, new species[2]
(Fig. 1)

Head.—Vertex obscurely roughened, elevated between eyes, obscurely covered with short, sparse hairs, trichobothrial hairs very long, prominent; length 2.10, width including eyes 1.95, anteocular length 1.26, antenniferous tubercle length 0.42, eye length 0.51, eye width 0.36, interocular space 1.17, bucculae most prominent as anteriorly projecting lobes, continuing as low carinae to near base of head, enclosing a tapering gular region; labium just exceeding posterior coxae, reaching base of abdomen, first segment just exceeding anterior margin of prosternum, segment lengths from base 1.95, 2.70, 1.92, 0.69; antennae clothed with short, appressed hairs, segments I, II, and III with a few longer hairs apically and segment I with three setae basally on medial surface, clypeus not reaching midpoint of segment I, segment lengths from base 1.26, 2.40, 1.98, 1.92.

Pronotum.—Sparsely clothed with long, erect setae, anterior lobe obscurely roughened and punctate, collar region and lateral explanate margins delimited by row of punctures, posterior lobe moderately punctate, distance between punctures from diameter of a puncture to three times this distance; medial length 2.70, greatest length 3.09, anterior and posterior margins deeply emarginate, anterior lobe prominent, swollen, lateral explanate carina of even width, about as wide as diameter of second antennal segment at middle, becoming wider between lobes, posterior lobe poorly differentiated

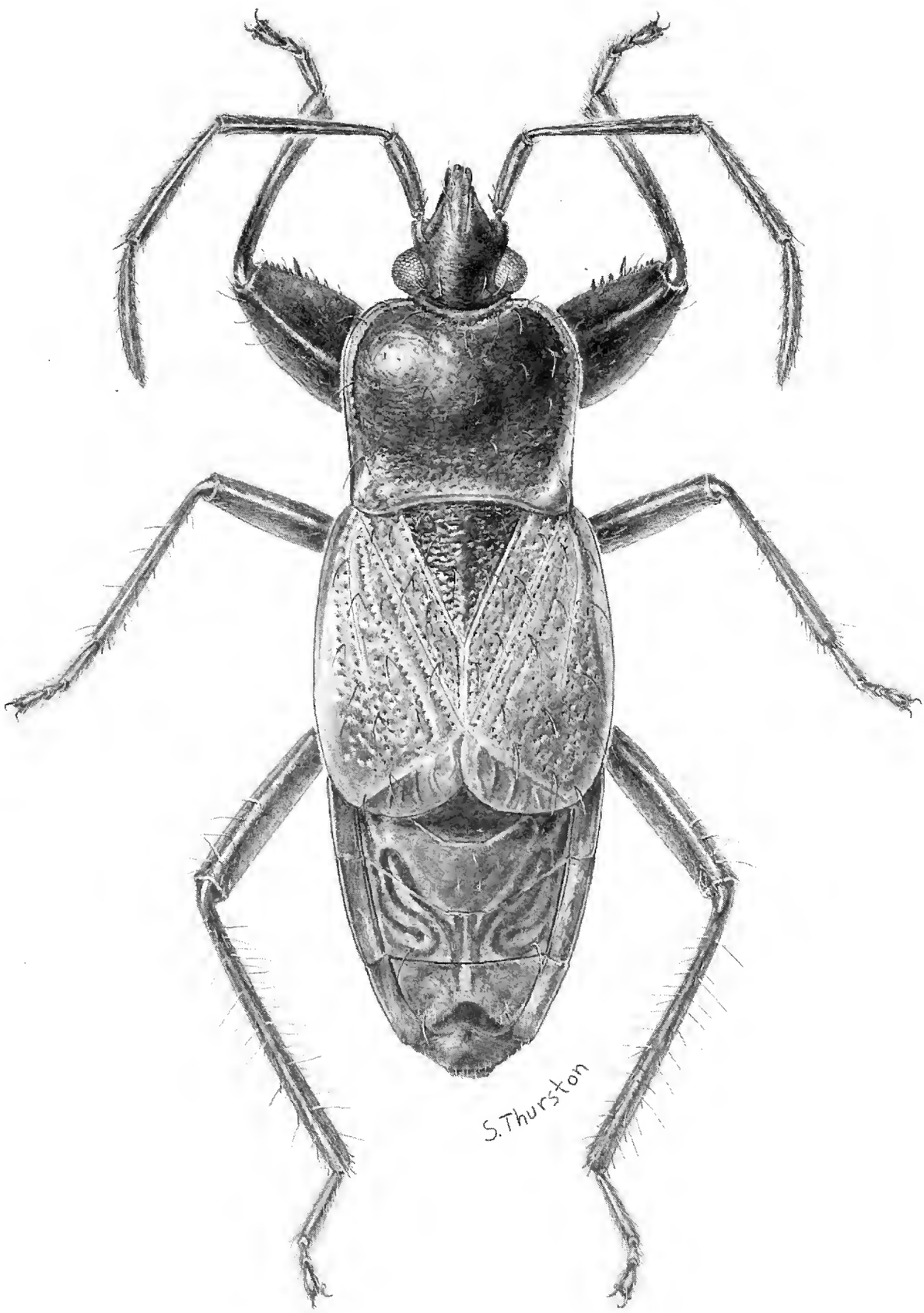

Fig. 1. *Eremocoris cupressicola* Ashlock, new species, dorsal view, holotype.

from anterior lobe, median length of anterior lobe 1.86, median length of posterior lobe 0.84, scutellum with surface curved down laterally, clothed with erect hairs and punctures like those on posterior lobe of pronotum, length 1.86, width 1.80.

Hemelytra.—Brachypterous, reaching abdominal segment V, clavus and corium with erect setae similar to those on pronotum, veins not evident, length of corium 4.35, length of claval commissure 1.20, membrane without evident veins, greatest width 1.86, greatest length 0.72.

Legs.—Fore femora greatly incrassate, width 1.35, length 3.39, armed beneath with two ranks of spines, with one large subapical spine on inner rank, accompanied by five small spines basally and four small spines apically, outer rank with three small apical spines. Fore tibia curved, with small tubercles on inner surface. Hind tibia with entire surface covered with long, erect setae three times as long as diameter of tibia.

Color.—Rather uniform dark reddish brown; acetabulae, coxae, lateral margins of hemelytra a little paler; tarsi yellow.

Length.—Female holotype 7.50; females, range 6.60 to 7.95, mean 7.52; males, range 6.90 to 7.05, mean 6.95.

Holotype female (California Academy of Sciences).—California, Marin Co., Carson Ridge, under bark of *Cupressus sargenti,* I-22-1957 (J. A. Chemsak).

Paratypes (California Academy of Sciences and the author's collection).—All California. 1 male, same data as holotype; 1 female, same data (P. D. Ashlock); 1 female, same data but I-9-1957 (J. A. Powell); 1 female, same locality but beating *Cupressus sargenti,* II-1-1958 (P. D. Ashlock); 2 females, same locality, V-6-1962 (C. W. O'Brien); 1 female, same locality, XI-15-1962 (J. A. Chemsak); 2 females, same locality, found dead under bark of dead *Cupressus sargenti,* VIII-9-1978 (P. D. Ashlock & E. Rogers); 1 male, same locality, habitat, date, collectors, but collected as nymph, emerged VIII-15-1978; 2 females, same locality, under board, IX-24-1963 (P. D. Ashlock & N. T. Davis); 1 female, Marin Co., Cypress Ridge, V-29-1920 (E. C. Van Dyke) [allotype of *Eremocoris semicinctus* Van Duzee]; 1 female, Marin Co., Fairfax, V-11-1919 (E. P. Van Duzee); 1 male, Alameda Co., Cedar Ridge, III-22-1931 (E. C. Van Dyke); 1 female, Sonoma Co., 1 mi NE Occidental, V-17-1964 (C. W. O'Brien); 1 male, Sonoma Co., 2 mi E Camp Meeker, XI-24-1962 (P. D. Ashlock); 1 female, same data (C. W. O'Brien); 1 female, Lake Co., St. Helena Creek, III-11-1951 (J. Helfer); 2 females, Lake Co., Highland Springs, V-10-1932 (R. L. Usinger); 1 female, Lake Co., Middletown, Putah Creek, V-11-1928 (E. P. Van Duzee).

In addition to the form of the brachyptery and the uniform color, distinctive features of *E. cupressicola* include the longest head of any North American member of the genus: the anteocular distance is greater than the interocular distance. The males have strongly curved fore tibiae, with sev-

eral short spines on the inner surface. The first of my specimens were collected under the bark of cypress trees in January, where the insects were probably overwintering. Beating the trees themselves has produced other specimens, and the best results have come from beating branches that have open cones with seeds. Presumably the bugs feed on the seeds, competing with *Kleidocerys obovatus* (Van Duzee) (Lygaeidae, Ischnorhynchinae), which is common in the same habitat.

In the twenties and thirties, such collectors as E. P. Van Duzee and E. C. Van Dyke referred to a specific locality in Marin County, California, as "Cypress Ridge," and some specimens of *E. cupressicola* bear this label. The correct name for this locality is Carson Ridge. The cypress forest lies past a locked gate at the end of Carson Road, which leaves the main road in the town of Woodacre.

Earlier keys (Barber, 1918; Torre-Bueno, 1946) to North American drymine genera combine this tribe with the Lethaeini and place the genus *Thylochromus* in the tribe Rhyparochromini. Slater and Baranowski (1978) do not distinguish tribes in their key, and omitted *Togodolentus* and *Thylochromus* because of the rarity of their species. Since no complete and correct key to genera has ever been provided, and since a better separation of *Eremocoris* and *Togodolentus* has been achieved, a new key to the six genera of Drymini found north of Mexico follows. The only other Western Hemisphere genus of Drymini listed in the Slater catalogue (1964) is *Scythinus* Distant, whose only species, *S. splendens* Distant, is not available for study. However, the key should be useful for Mexico as well. The most recent characterization of the Drymini is that of Sweet (1967), and the group can be recognized by the two trichobothria (not three) that are placed anteriorly on abdominal segment five.

Key to the Genera of Drymini of America North of Mexico

1. Lateral margin of pronotum angulate, not foliaceously expanded; brachypterous forms without a trace of membrane; Pacific Coast states ..... *Thylochromus* Barber
   Lateral margins of pronotum foliaceously expanded at least between anterior and posterior lobes; brachypterous forms with obvious hemelytral membrane 2
2. Ventral abdominal sutures straight and reaching lateral margins; flattened, cone-living bugs ..... *Gastrodes* Westwood
   Ventral abdominal suture IV–V curving anteriorly and not reaching lateral abdominal margins; robust, mostly ground-living bugs 3
3. First antennal segment shorter than distance between eyes; apex of clypeus reaching at least to middle of antennal segment I 4
   First antennal segment longer than distance between eyes; apex of clypeus not reaching middle of antennal segment I 5

4. Antennae densely covered with semierect hairs that are longer than diameter of segments; east of Rocky Mts..... *Drymus* Fieber
   Antennae with only an occasional erect hair, most hairs appressed and shorter than diameter of segments ..... *Scolopostethus* Fieber
5. Bucculae extending posteriorly as carinae only as far as level of anterior margin of an eye, enclosing a parallel-sided gular region; width of lateral pronotal expansions at middle of anterior lobe greater than diameter of antennal segment II measured at its middle; California ..... *Togodolentus* Barber
   Bucculae extending posteriorly as carinae to base of head, enclosing a gular region that narrows posteriorly; width of lateral pronotal expansions at middle of anterior lobe not wider than diameter of antennal segment II measured at its middle ..... *Eremocoris* Fieber

Acknowledgments

I am grateful to Dr. Paul H. Arnaud, California Academy of Sciences, for the loan of specimens of *E. cupressicola,* and for permitting me to study Van Duzee's types of the genus *Eremocoris*. The excellent illustration was executed by Mr. S. Thurston, University of Connecticut, Storrs.

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Footnotes

[1] Contribution no. 1627 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045.

[2] All measurements in millimeters.

PAN-PACIFIC ENTOMOLOGIST
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A NEW CALIFORNIA SPECIES OF *PODABRUS* (COLEOPTERA: CANTHARIDAE)

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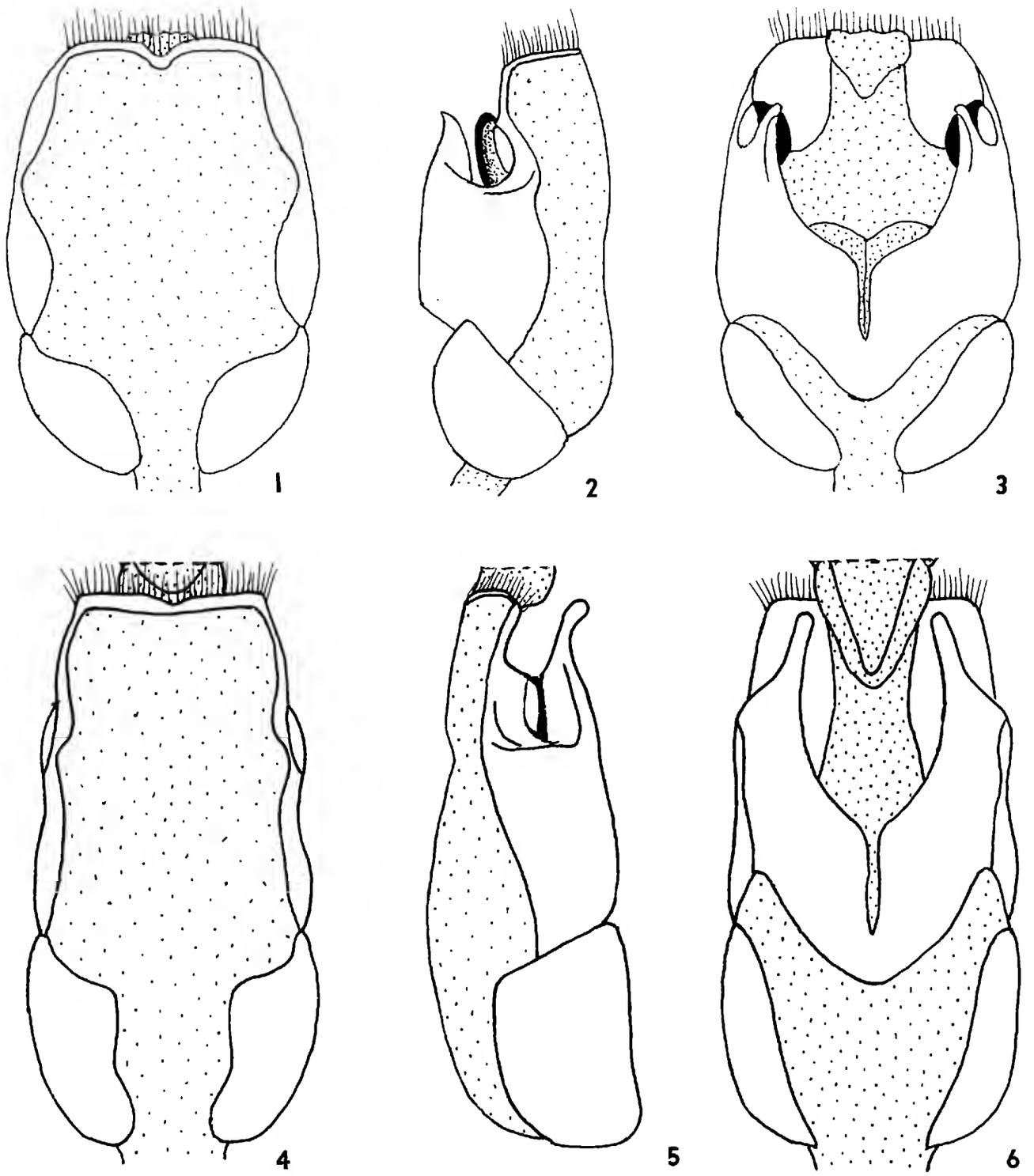
The following new (to science) species is named for its principal collector: Daniel K. Young, Michigan State University, an avid student of the Pyrochroidae and of the pedilid genus *Pedilus*.

Podabrus youngi, new species

Head pale flavous, becoming black behind on the dorsal surface, black area commencing at anterior margin of eyes and deeply arcuately receding medially to posterior margin of eyes, behind eyes extending along lateral median line of neck, not attaining base of neck; apical margin of last segment of maxillary palpi narrowly infuscate; labial palpi piceous; antennae becoming infuscate beyond middle of fourth segment. Pronotum and scutellum flavous. Elytra black. Head, prothorax beneath and legs flavous. Mesothorax and metathorax black. Abdomen piceous. Pubescence fine, short and sparse, aureous on pale portions, black on black portions.

Male.—Head shining, as wide as pronotum, moderately rapidly narrowed behind eyes, eyes moderately large and prominent. Clypeus impunctate save for fine close punctures along anterior margin. Head finely sparsely puntured between eyes, punctures separated by two to three times their diameters, a little more coarsely punctured behind, becoming rather coarsely rugose punctate on neck; an evident arcuate interocular ridge extending from eye to eye; apical segment of maxillary palpi elongate triangular, twice as long as wide, widest medially, inner side straight, apical side arcuate, outer side shallowly concave; antennae slender, extending to about apical third of elytra, third segment shorter and thicker than second, fourth segment half again as long as third, intermediate segments about four times as long as wide. Pronotum shining, slightly transverse, widest medially, lateral margins arcuate from obliquely angulate hind angles to rounded anterior angles, disc broadly explanate at anterior angles, broadly and rather deeply reflexed at posterior angles, anterior margin shallowly concave, posterior margin more deeply concave and deeply guttered, convexities moderately high and unevenly reniform in shape, median longitudinal impressed line feebly indicated and not eroded, discal punctures fine and sparse. Scutellum shining, finely sparsely punctured, subtriangular, sides straight, apex sharply rounded. Elytra shining, parallel sided, about three times as long as their width



Figs. 1–3. *Podabrus sierrae*. Fig. 1. aedeagus of male, dorsal view. Fig. 2. same, lateral view. Fig. 3. same, ventral view. Figs. 4–6. *Podabrus youngi*. Fig. 4. aedeagus of male, dorsal view. Fig. 5. same, lateral view. Fig. 6. same, ventral view.

at the humeri, finely rugose punctate basally, becoming more coarsely so apically. Thorax shining beneath, pubescence of mesothorax and metathorax cinereous, rather long and somewhat depressed. Abdomen dull, pubescence shorter and more dense than on mesothorax and metathorax. Legs slender and long, protibiae and metacoxae not sexually modified, all claws broadly cleft. Aedeagus as in Figs. 4–6. Length (head extended) 14 mm.

Female.—Similar to male. Head narrower than pronotum, eyes smaller and less prominent. Pronotum more transverse, sides more rounded. Length (head extended) 15 mm.

Holotype male and allotype female.—California, Mariposa County, Sierra National Forest, Summerdale Campground, 11–15 June 1973, D. K. & D. C. Young, in the collection of the California Academy of Sciences at Mr. Young's request. 208 paratypes with the same data. In a letter, Mr. Young noted that they were on the foliage of willows. Paratypes also from the following California localities: Tuolumne Co.: Strawberry (11 miles north), 24-VI-51, R. W. Morgan; Strawberry, 12-VII-52, M. Cazier, W. Gertsch & R. Schrammel; Dardanelle, 13-VII-52, M. Cazier & W. Gertsch; Crocker Station, 6 mi s. of Mather, 12-VI-61, C. D. McNeill; Mather, 9-VI-61, D. R. Miller; Long Barn, 16-VI-61, R. R. Snelling; Miguel Meadows, Swamp Lake, 24-VI-76, black light, R. P. Allen. Alpine Co.: 4 mi w. of Woodfords, 25-VI-61, A. S. Menke; Woodfords, 28-VI-62, W. E. Simonds; Hope Valley, 18-VII-48, R. C. Bynum; Markleeville, 2-VII-50, collected at light, W. C. Day. Eldorado Co.: Fallen Leaf Lake, 10-VII-35, 6500 feet, F. E. Blaisdell; Tallac, VII-99, Van Dyke; Tahoe, Tallac, 5-VII-15, E. P. Van Dyke. Madera Co.: Oakhurst, 5-VI-42, on *Ceanothus,* Arthur J. Waltz; Bass Lake, 14-VI-34. Mono Co.: 4 mi e. of Monitor Pass, 24-VI-62, C. D. McNeill. Mariposa Co.: Yosemite Valley, 23-VI-21, VanDyke coll.; Yosemite Valley, Mariposa Grove, 30-VI-37, 6500 feet, E. Herald. Nevada Co.: Cisco, VI. San Bernardino Co.: San Bernardino Mts., 2-VII-17, 7500 feet.

Some of the paratypes are in the collection of the author and the others are to be deposited in various collections, some of which include: Daniel K. Young; Michigan State University, East Lansing; California Department of Food and Agriculture, Sacramento; California Academy of Sciences, San Francisco; Oregon State University, Corvallis; Museum of Comparative Zoology, Harvard University; National Museum of Natural History, Washington, D.C.

The following California localities are also represented but could not be satisfactorily placed as to county: Sugar Pine, 21-VII-33, 25-VII-33, E. Schiffel. There is more than one Sugar Pine in California. Myers, 28-VI-30, A. T. McClay. This may be a misspelling of Meyers, Eldorado County. Deerpark Inn, July. I was finally able to find a Deerpark, Placer County in a 1938 Shell Oil Company road map of California.

In Fall's (1928) review of *Podabrus* this species would key to *P. sierrae* Fall. In all of the specimens of *P. sierrae* examined, the black of the back of the head always extends to and includes the base of the neck. The scutellum is black. The male aedeagus is less elongate and the ventral lobes are less strongly produced (Figs. 1–3).

In *P. youngi* the coloration of the head is quite variable. The black area may be reduced to a rather narrow arcuate interocular fascia. It may be

expanded beneath to nearly attain the gular sutures. However, in the more than 200 specimens examined, the black never does attain the base of the neck. The scutellum is flavous.

Literature Cited

Fall, H. C. 1928. A review of the North American species of *Podabrus*. Entomol. Amer. 8(new series)2: 65–103.

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SCIENTIFIC NOTE

NOTES ON THREE OREGON LEPTURINE CERAMBYCIDAE (COLEOPTERA)

Cortodera militaris constans L. & C.—Linsley and Chemsak (1972, Univ. Calif. Publ. Entomol. 69: 109–111) segregated *C. militaris* into three subspecies, listing only the nominate form as occurring in the Pacific Northwest. Concurrently, they described the subspecies *C. m. constans* from northeastern California, which might suggest that this taxon also inhabits adjacent regions of Oregon. Collections verifying this assumption have recently been made in Lake Co.: (6 ♂♂, 3 ♀♀) 3.3 and 5.4 mi SE Quartz Mt., VI-16-1977 on *Ranunculus occidentalis* Nutt. (R. L. Penrose); (3 ♂♂, 15 ♀♀) 14.8 mi N. Lakeview, VI-14-1977 on *R. occidentalis* and *Potentilla gracilis* Dougl. ex Hook. (R. L. Penrose); (13 ♂♂, 30 ♀♀) VI-8-1978 on *R. occidentalis* (R. L. Penrose and R. L. Westcott). Although these specimens are clearly best placed with *constans* (on the basis of anatomical similarities and geographic proximity), they exhibit more variation in elytral coloration than is evident in Modoc County material. The name *constans* was given on the basis of the uniformity of the type series, i.e., "all individuals black with red humeri." In the Lake County material cited above, 60 specimens (86%) are typical *constans,* 9 (13%) have elytra brown/vittate and 1 (1%) is wholly black. Inclusion of Oregon populations would therefore require a redefinition of *constans* to encompass predominately black populations in which the red humeral condition is *usually* expressed. It should also be noted that four of the six specimens from Quartz Mt., in marked contrast to other Lake County specimens, have the reddish mark vaguely defined and restricted to the humeral angle. This reduction in maculation size, combined with the occurrence of a wholly black individual could indicate that transitional populations between *constans* and typical *militaris* remain to be discovered in the Klamath Basin. Although much remains to be done to unravel the population structure of this species, specimens at hand suggest a divergence in melanistic tendencies on opposite sides of the Cascade Range. Whereas *constans* is typically melanic, black individuals comprise only 20% of the beetles examined from western Oregon. Another interesting phenomenon is found in the distribution of local populations with red and black individuals within the range of the nominate subspecies. All bicolored specimens seen are from Washington (Tacoma, Olympia and Chehalis), and Linsley and Chemsak's statement that black *militaris* tend to have reddish humeri would seem to be valid only as regards specimens from the northern portions of the subspecies range.

Typocerus serraticornis Linsley and Chemsak.—Recently described from specimens collected in Nevada, Utah, New Mexico and Idaho (1976, Univ.

Calif. Publ. Entomol. 80: 69), this species also occurs in southeastern Oregon. A series was collected in Harney Co., Little Cottonwood Creek, VI-6-1978 (R. L. Penrose and R. L. Westcott). Beetles were sporadically abundant in the flowers of *Sphaeralcea grossulariaefolia* (Hook. and Arn.) Rydb. (currant-leaved desert mallow) which was growing intermixed with the larval host, Sand Dropseed (*Oryzopsis hymenoides* (Roem. and Schult.) Ricker). Occasional *Typocerus* were also taken on flowers of *Eriogonum ovalifolium* Nutt. An additional collection was made 22 mi NW of Denio Junction, Humboldt Co., Nevada, on June 7. At this site, beetles were quite abundant but very localized, nearly all having been encountered on a single 165 square meter area of sand, covered almost exclusively with *O. hymenoides*. They were observed flying slowly about, and sitting and mating on this grass. Occasionally, females were noted crawling on the surface of the sand around the plant bases in search of oviposition sites. Larvae were found at both localities boring in culm bases, below the soil surface, indicating at least a two-year life cycle.

Ortholeptura obscura (Swaine and Hopping).—There have been but three prior references to this species, all of which are descriptive (Swaine and Hopping, 1928, Nat. Mus. Canada Bull. 52: 56; Hatch, 1971, Univ. Wash. Publ. Biol. 16: 132; Linsley and Chemsak, 1976, Univ. Calif. Publ. Entomol. 80: 133). These references are apparently based upon a single male and female specimen. The literature has been reflective of specimen availability and I have seen only two specimens of *obscura* (both from northeastern Oregon) in Pacific Northwest collections during the past decade. Due to the rarity of this species, and the absence of any published biological information, the following observations are presented. On July 25, 1978, five specimens were collected at Wallowa Lake State Park, Wallowa County, Oregon, as follows: 1 ♂ was attracted to white light; 1 ♀ was found clinging to the underside of a freshly fallen branch of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas Fir); 1 teneral adult ♂ and 2 pupae, 1 ♂, 1 ♀, were collected from pupal cells in the dry, hard outer sapwood near the top of an old Douglas Fir stump. A single ♂ was swept from foliage of Snowberry, *Symphoricarpos* sp. at Field Spring State Park, Asotin County, Washington, VIII-30-1966 by R. L. Westcott.

Special thanks is extended to Dr. J. D. Lattin, Curator, Oregon State University Entomological Collection, Corvallis, for permission to study specimens of *C. militaris* present in the recently acquired M. Hatch Collection.

Richard L. Penrose, *Oregon Department of Agriculture, Salem, Oregon 97310.*

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